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THE FISH AND CRUSTACEAN ASSOCIATES OF THE SEA ANEMONES *URTICINA LOFOTENSIS* AND *URTICINA PISCIVORA*

BY

©

JOEL K. ELLIOTT

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND
RESEARCH IN PARTIAL FULFILMENT OF THE REQUIREMENTS
FOR THE DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

(SPRING) (1987)

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled THE FISH AND CRUSTACEAN ASSOCIATES OF THE SEA ANEMONES *URTICINA LOFOTENSIS* AND *URTICINA PISCIVORA* submitted by Joel Kenneth Elliott in partial fulfilment of the requirements for the degree of Master of Science.

(Co-Supervisor)

T.E. Reimchen

W.G. Evans

A.N. Spencer

Date: October 28, 1986

DEDICATION

This thesis is dedicated to the memory of my supervisor, Dr. D. M. Ross, who passed away on the 13th of February, 1986. His enthusiasm for the study of the behavior and ecology of marine invertebrates strongly influenced my interests in marine biology. His encouragement, support, and paternal guidance gave me the desire and confidence to continue my research at the graduate level. I am very thankful and proud to have had the opportunity to be a student of Dr. Ross's, and I will be forever grateful to him for his influence on my life and career.

ABSTRACT

An assemblage of four fish species and three crustacean species were found to associate with anemones in Barkley Sound, Vancouver Island, British Columbia. Small individuals (<6 cm total length) of the fish *Oxylebius pictus* had a close association with *Urticina lofotensis*. Large individuals of *O. pictus* were found intermittently with either *U. lofotensis* or *U. piscivora*, with most adults (>12 cm total length) sheltering in cracks and crevices. Other small fishes, *Artedius harringtoni*, *Jordania zonope*, and *Coryphopterus nicholsii* were only intermittent associates of anemones, along with the crab *Scyra acutifrons* and the shrimp *Heptacarpus kincaidi*. All of these species were facultative associates. The copepod *Doridicola sunnivae* had an obligate relationship with *U. lofotensis*.

Field studies revealed that the number of organisms associating with anemones varied spatially, temporally, and with respect to characteristics of the associates and their hosts. Spatial variation in the association patterns were related to differences in the population densities of each species under various conditions of wave exposure, depth, habitat structural complexity, and abundance of predators. More fish associated with anemones at night, and crabs and shrimps were found with anemones mostly during the day. Seasonal variation in the associations were related to changes in environmental variables, patterns of recruitment, activity levels of the associates, and predator abundance. Of seven species of large anemones at the study sites, most associates were found with *U. lofotensis*. The size, orientation, and tentacular adhesive force of the anemones were important parameters affecting host specificity.

The major benefit of the relationships for the associates was protection from predators. Associates which could acclimate to the anemones also received nutritional benefits. *Doridicola sunnivae* and *Scyra acutifrons* fed on the mucus and possibly tissues of *U. lofotensis*. Large crabs also stole food from the coelenteron of their hosts. *Oxylebius pictus* fed on *D. sunnivae*. The net effect of the associations on the anemones appeared to be minimal, and most of the associates were probably commensals. The characteristics of these associations were compared to predictions based on evolutionary models of the conditions under which different types of symbioses should evolve.

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INTRODUCTION

Ecologists have historically centered their efforts on investigating antagonistic interactions between species (i.e., competition, predation, and parasitism), and have attributed observed population and community patterns to these processes (Connell, 1983; Schoener, 1983; Sih et al., 1985; May and Seger, 1986). The study of beneficial interactions between species (i.e., mutualism and commensalism) has been neglected throughout most of the 20th century (Boucher et al., 1982; Boucher, 1985), but recently has "emerged as a strong and active discipline within ecology" (Addicott, 1984). The prevalence and importance of these interactions is now being recognized, and ecologists are continually describing novel ways in which organisms benefit each other. Despite the surge of interest in this topic, the terminology used in describing positive interactions has yet to be agreed upon. The term "symbiosis" has caused much confusion. Some scientists prefer the meaning of symbiosis to contrast with that of parasitism, but current opinion has reestablished de Bary's (1879) original meaning of symbiosis as a living together of dissimilar organisms (Henry, 1966; Starr, 1975; Lewis, 1985). This definition disregards any advantages or disadvantages to the participants, and encompasses parasitism, commensalism, and mutualism. It also does not require that the organisms have some type of physiological integration (cf. Boucher et al., 1982) or prolonged period of association (Lewis, 1985).

Mutualism is defined as any interaction in which two or more species reciprocally benefit from the presence of the other species; commensalism is any interaction that benefits one species without affecting the other; and parasitism exists when one species is benefitted and the other is harmed by the association. These interactions can be further defined by many different factors as described by Addicott (1984) and Lewis (1985). The major criteria discussed in this study are the degree to which an interaction is necessary for the survival of each species (facultative or obligate), the kinds of benefits (e.g., protection, feeding, cleaning) or detriments (e.g., feeding on host tissue), the duration of the interactions (intermittent to permanent), the strength of the interactions (variable, constant), and the mode of transfer of benefits or detriments (indirect, direct).

Symbioses are often difficult to distinguish in practice, because of shifts in the nature of the interactions over temporal and spatial scales (Janzen, 1985), and the difficulty in obtaining unequivocal demonstrations of benefit or detriment to the partners in a relationship (Addicott, 1984). In fact, some systems which have appeared to be either parasitic or commensal have on closer analysis turned out to be mutualistic under certain environmental conditions (e.g., N. G. Smith, 1968; Glynn, 1976, 1983; W. L. Smith, 1977). This makes it particularly difficult to apply labels to symbioses in which the costs and benefits to the partners are not straightforward. Especially evident is the labelling of many small organisms as parasites, when neither harm nor benefit to the host has been demonstrated. Measurements of the net costs and benefits to the partners in an association under a specific set of environmental conditions are required before an association can be described as being parasitic, commensal, or mutualistic. This involves experimental manipulations and appropriate measurements of fitness for both species in the presence and absence of the other. However, these criteria are often very difficult to satisfy for many associations in which costs and benefits are obscure or indirect (Addicott, 1984).

Many examples of beneficial interactions between organisms have now been documented in both terrestrial (Janzen, 1985) and aquatic ecosystems. Mutualistic and commensal interactions are very common in marine environments (Dales, 1957; Henry, 1966; Vernberg, 1974; Zann, 1980; Vermeij, 1984), especially associations involving cnidarians (cf. Ross, 1974, 1983). Cnidarians are hosts to a wide variety of organisms: intracellular algae and dinoflagellates (Muscatine and Porter, 1977; Cook, 1985), mollusks (Shimek,1981), phoronids (Emig et al., 1972), hermit crabs

(Ross, 1971, 1974, 1983, 1984), amphipods (Vader and Lønning, 1973); and copepods, crabs, shrimps, and fishes (to be discussed). Cnidarians have two major attributes which make them ideal hosts for other taxa: 1) they provide shelter from predators because they possess cnidae (nematocysts and spirocysts), organelles which are very effective in deterring predators (Ross, 1971), 2) they produce large amounts of mucus which can be utilized as a food resource (Glynn, 1976, 1983). The symbionts of cnidarians have evolved many different behavioral, physiological, and morphological adaptations in order to take advantage of these benefits.

A classic example of mutualism involving cnidarians is the association between clownfishes (genera *Amphiprion* and *Premnas*) and anemones in the Indo-Pacific (Mariscal, 1966, 1970; Allen, 1975; Fricke, 1975; Ross, 1978; Fautin Dunn, 1981). The major benefit of the association for the fish is protection from predators, which would be killed or injured if they tried to pursue the clownfish into the tentacles of its host anemone (Mariscal, 1966, 1970; Allen, 1975). Some species of anemones benefit from the clownfishes' behavior of selectively chasing away butterfly fishes which are known anemone predators (Fricke, 1975). These associations are usually obligate for both the fishes and anemones, but facultative associations between other species of fishes and anemones have also been reported from many tropical areas Stevenson, 1963; Schlichter, 1970; Smith, 1973; Colin and Heiser, 1973; Gendron and Mayzel, 1976; Hanlon and Kaufman, 1976; Hanlon et al., 1983) and they appear to be relatively more common than their obligate counterparts.

Facultative mutualisms and commensalisms are considered to be less obvious because of reduced specificity or intermittent association (Addicott, 1984). The obscure nature of these interactions is probably why few facultative fish-anemone associations have been reported until recently. Hanlon and Kaufman (1976) predicted that the number of reported fish-anemone associations would increase considerably once more effort was spent looking specifically for them. An investigation of the fish associates of Caribbean anemones has resulted in the discovery of more than 30 species of reef fishes as facultative associates of anemones (Hanlon et al., 1983). Relatively little is known of the ecology of these associations in comparison to obligate associations, and the costs and benefits to the partners in these facultative relationships have not been thoroughly examined.

Cnidarians are also known to harbor a variety of crustaceans. Much research has been done on the crab and shrimp associates of corals (Knudsen, 1967; Patton, 1974; Abele, 1976; Glynn, 1976; Edwards and Emberton, 1980; Gotelli and Abele, 1983; Gotelli et al., 1985), but relatively few detailed studies have been done on the crustacean associates of sea anemones (as stated by Stanton, 1979; Fautin Dunn, 1981). An extensive behavioral and ecological study has been conducted on the obligate alpheid shrimp associates of Caribbean anemones (Knowlton, 1978, 1980), and some population and community studies have been done on the facultative crustacean associates of sea anemones (Herrnkind et al., 1976; Stanton, 1976, 1979). Most of the work on crustacean associates has been carried out on large species, and virtually nothing is known about the many species of copepods which are found on anemones (Gotto, 1979; Humes, 1982).

Different species of associated fishes and crustaceans vary in their patterns of host specificity. The characteristics which make a certain host good or bad (size, shape, etc.) have not been investigated, and require study. Both fishes and crustaceans often associate with the same host cnidarians. Since most of these associates are highly territorial, studies of interactions between associates have centered on intraspecific and interspecific competition for hosts. These studies have indicated that competition (Preston, 1973; Fautin, 1984; Huber and Coles, 1986), and host specificity (Knowlton and Keller, 1986) are important in explaining negatively correlated distribution patterns. Resource partitioning (Stanton, 1976; Lassig, 1977), and communication between associates (Lassig, 1977; Vannini, 1985) have been shown to allow coexistence of different species on the same hosts. The occurrence and potential effects of predation by one species on the abundance or presence of another associated species has not been thoroughly addressed for relationships involving actinians. This is especially evident for interactions between fishes and small crustacean associates such as copepods.

Most studies of symbioses involving anemones have attempted to determine the mechanism which allows the fish or crustacean to live amongst the tentacles of its host without being stung. It is now known that the symbiont gains protection through a process called acclimation. At the start of acclimation the symbiont is stung upon intial contact with the tentacles, but after repeated contacts the fish or crustacean is no longer stung (Mariscal, 1971; Levine and Blanchard, 1980). During acclimation the mucous coating of the symbiont is altered, allowing it to contact the anemone without being recognized as foreign material (Mariscal, 1971; Lubbock, 1980). However, the biochemical alteration which occurs during acclimation is still unknown (Brooks, 1984). Both biochemical and immunological studies will probably be needed to determine the nature of this protection.

Despite the large amount of work done on the fishes and crustaceans in these relationships, relatively little work has been done on the anemones. A major problem has been the identification of host anemones, and in some studies the species of anemone is not even mentioned or no indication is given of how the identity was determined (Fautin Dunn, 1981). Detailed life history and ecological studies need to be conducted on anemones to obtain a better understanding of their role in these associations. The work of Ross (1973, 1974, 1983) has shown that we can no longer assume that the anemone is always a passive partner in symbiotic associations, but that they have the ability to evolve complex behaviors and morphological adaptations in response to various selective pressures. Alternatively, if the anemones do not appear to have coevolved with their symbionts, the question remains as to why they have not.

Some kinds of obligate mutualisms occur more frequently in tropical and subtropical ecosystems than in temperate and arctic ecosystems (May, 1976). Many examples in the marine environment suggest that there is a latitudinal decline in the number of intimate associations from the equator to the poles (Vermeij, 1984). Obligate fish-anemone associations follow this biogeographical distribution pattern and are known exclusively from tropical waters. Associations between crustaceans and cnidarians are also common in tropical regions, but their occurrence in temperate waters is considered to be rare (Bruce, 1976). Facultative associations, which involve cnidarians as hosts, are found in both tropical and temperate regions. There have been considerably more reports from tropical regions, however (review by Stanton, 1979), and the only facultative associations which have been studied in temperate waters involve the fish (Abel,1960), crab (Hartnoll, 1970; Weinbauer et al., 1982; Wirtz and Diesel, 1983; Diesel, 1986) and copepod (Briggs, 1976) associates of *Anemonia sulcata* Penn. in the Mediterranean and northeast Atlantic waters. Two species of shrimps have been reported to associate with anemones in the northeast Pacific (Hoffman, 1967; Butler, 1980), but population studies have yet to be conducted. The relatively small amount of work which has been done on the ecology of subtidal, temperate sea anemones may account for the paucity of reported associations.

It is clear that many questions remain to be answered about associations involving cnidarians as hosts. This is especially evident for facultative associations between actinians and other organisms. Basic ecological work is needed to describe the population and community dynamics of hosts and their associates, and experimental studies are also needed to measure the costs and benefits to the partners in the associations. The prevalence and diversity of associations involving cnidarians make them especially useful for the investigation of other questions which are central to the study of symbioses: the basis of host specificity, biogeographical distribution patterns, competition and predation within symbiotic systems, the effects of beneficial interactions on population density and stability, and the evolution of symbiotic relationships.

The system discussed here involves the associations of four species of fishes and many crustaceans with certain species of anemones in the temperate waters of the northeast Pacific. The initial study was concerned with investigating the association between the fish *Oxylebius pictus* and and the anemones *Urticina lofotensis* and *U. piscivora*. However, after a preliminary examination of this association it became apparent that other fishes and crustaceans were also found with the anemones. The study was then extended to include an examination of these interactions. The purpose of the study was to describe the population and community structure of host anemones, their associated organisms, and their predators in a number of habitats over 18 months. Since the fishes and crustaceans both shared the same host species of anemones, the interactions between associates could be examined. The presence of many species of anemones in the area also allowed study of the possible basis of host specificity by examining differences between host and non-host species. The associations appeared to range from parasitic to mutualistic relationships and differ with respect to the modifiers previously outlined. Having a range of associations made the system especially amenable to a comparative examination of the selective pressures which may have caused the different types of associations to arise.

The approach taken for the investigation was to first obtain knowledge of the natural history, population biology, and behavior of the organisms from field and laboratory studies in order to identify the important components of their environments (Andrewartha and Birch, 1984). Secondly, experiments and manipulations were conducted to test hypotheses formulated to explain certain distribution and abundance patterns which became apparent after initial studies.

Natural history of anemones and their associates

Urticina (=*Tealia*) *lofotensis* and *U. piscivora* occur in exposed, rocky subtidal habitats on the Pacific Coast of North America from the California Channel Islands to southern Alaska (Hand, 1955; Sebens and Laakso, 1978). In Barkley Sound, these two *Urticina* species are generally most abundant in exposed habitats, and are rare to absent in calm protected waters (Elliott et al., 1985). Population densities of *Urticina lofotensis* are highest in shallow water (0-15 m) and groups of four or five anemones are commonly found in individual cracks and crevices. *Urticina piscivora* is most abundant in deeper water (3-25 m) on vertical rock walls and on tops of boulders (Sebens and Laakso, 1978; Elliott et al., 1985). The anemones feed on small, motile marine invertebrates and *U. piscivora* also feed on small fishes (Sebens and Laakso, 1978; Elliott and Warren, in prep.). Both species are dioecious, with peak spawning of *U. lofotensis* occurring in December (Wedi and Fautin Dunn, 1983). Little is known about recruitment and other population characteristics of these species.

The painted greenling, *Oxylebius pictus*, is a small hexagrammid fish (up to 25 cm total length) found in shallow rocky habitats between 5-30 m in depth in the northeastern Pacific Ocean (Demartini and Anderson, 1980). It occurs from Point San Carlos, Baja California, to the British Columbia-Alaska border (Hart, 1973; Peden and Wilson, 1976). The distribution of *O. pictus* is sporadic north of the Strait of Georgia in British Columbia and it is rare to absent from the Strait of Juan de Fuca and nearshore rocky areas of the northernmost outer Washington coast (Demartini and Anderson, 1980). The only population studies which have been done on this species are by Demartini (1976) and Demartini and Anderson (1980), who examined populations in the Puget Sound area, Washington State, and in Monterey Bay, California. These populations are not associated with sea anemones. In these areas, *O. pictus* selectively feeds on crustaceans and other epibenthic organisms when it is active from April to November. Adult fish are territorial and males defend egg masses spawned in high relief rocky areas during spring and summer reproductive periods. The eggs hatch after 16-24 days, and the larvae spend 1-3 months in the plankton. Once recruited to shallow rocky reefs, small post-settlement fish are demersal, solitary, and non-migratory. Juveniles have small home ranges and occupy reef areas with females outside of male territories.

The other fish species found to associate with anemones in this study are all small bottom-dwelling fishes. Two sculpin species, *Artedius harringtoni* and *Jordania zonope*, occur from Alaska to California. They are most abundant in exposed, subtidal, rocky areas (Hart, 1973; Eschmeyer et al., 1983). Both of these fishes are territorial, sheltering in holes and crevices or with anemones. Populations of these species have been studied in Barkley Sound by Gascon (1982). The goby, *Coryphopterus nicholsii*, occurs from northern British Columbia to California (Hart, 1973; Eschmeyer et al., 1983). It is usually found in protected sand-boulder areas where it shelters in holes under rocks. Males guard nest sites from April to October. The biology of this species has been studied in Barkley Sound by Cole (1982).

Many crustacean species have been observed in association with *Urticina*. Copepods in the genus *Doridicola* have been reported on all *Urticina* species (Lønning and Vader, 1984); *D. sunnivae* is found on *U. lofotensis*, and *D. confinis* is found on *U. piscivora* . These copepods are host specific, living on the column and tentacles of the anemones where they probably feed on host mucus and tissue (Lønning and Vader, 1984). The copepods on *U. lofotensis* are dimorphic in color; some are red and others are white. They spend their entire lives on their host anemones, except for a series of planktonic naupliar stages. The copepods are short lived, with many generations per year. They have a high fecundity, females releasing hundreds of nauplii from paired egg sacs at regular intervals.

The shrimps *Heptacarpus kincaidi* and *Lebbeus grandimanus*, and the crab *Scyra acutifrons*, have also been observed with many species of anemones (Hoffman, 1967; Butler, 1980; Elliott, 1985). They are most commonly observed next to the columns of anemones, but *L. grandimanus* has also been observed in the tentacles. Little is known of the population biology of these species.

MATERIALS AND METHODS

Study sites

Population distributions and abundances of anemones and their fish and crustacean associates were examined using SCUBA throughout Barkley Sound near the Bamfield Marine Station, Bamfield, Vancouver Island, British Columbia (Fig. 1). Long term population studies were done at Ohiat Islet and Blackfish Islet. Experimental manipulations were conducted at the mouth of Bamfield Inlet (=Harbor Limit). Ohiat Islet is an exposed site open to oceanic swell. The study area consisted of a sloping solid rock substratum to a depth of approximately 20 m, which leveled off into a mixed boulder sand flat (Fig. 2). This site is also described in studies by McElderry (1979) and Fletcher (1981). Blackfish Islet is a semi-protected site which is separated from Helby Island by a shallow (6 m) sand flat area (Fig. 3). On the southeast side of the the islet the topography changes from a rock boulder substratum to a steep, solid rock slope which extends to depths beyond 50 m. A dense assemblage of sessile marine invertebrates and kelp beds of *Nereocystis luetkeana* and *Macrocystis integrifolia* are found in shallow water at Ohiat and Blackfish Islets, respectively. The Harbor Limit site is a protected area exposed to little wave action compared to either Blackfish or Ohiat Islets. There is a *Macrocystis integrifolia* bed in shallow water, and a rock boulder substratum extends to a depth of approximately 10 m, where a sand bottom begins.

Population biology

Permanent study areas at Blackfish and Ohiat Islets were surveyed to determine population densities and distributions of resident anemones, and to produce a map of the general topography of the sites. Transect lines were anchored with concrete weights at the shore in shallow water (approximately MLLW), and placed perpendicular to the shoreline to a depth of approximately 20 m. A 1 m^2 quadrat was

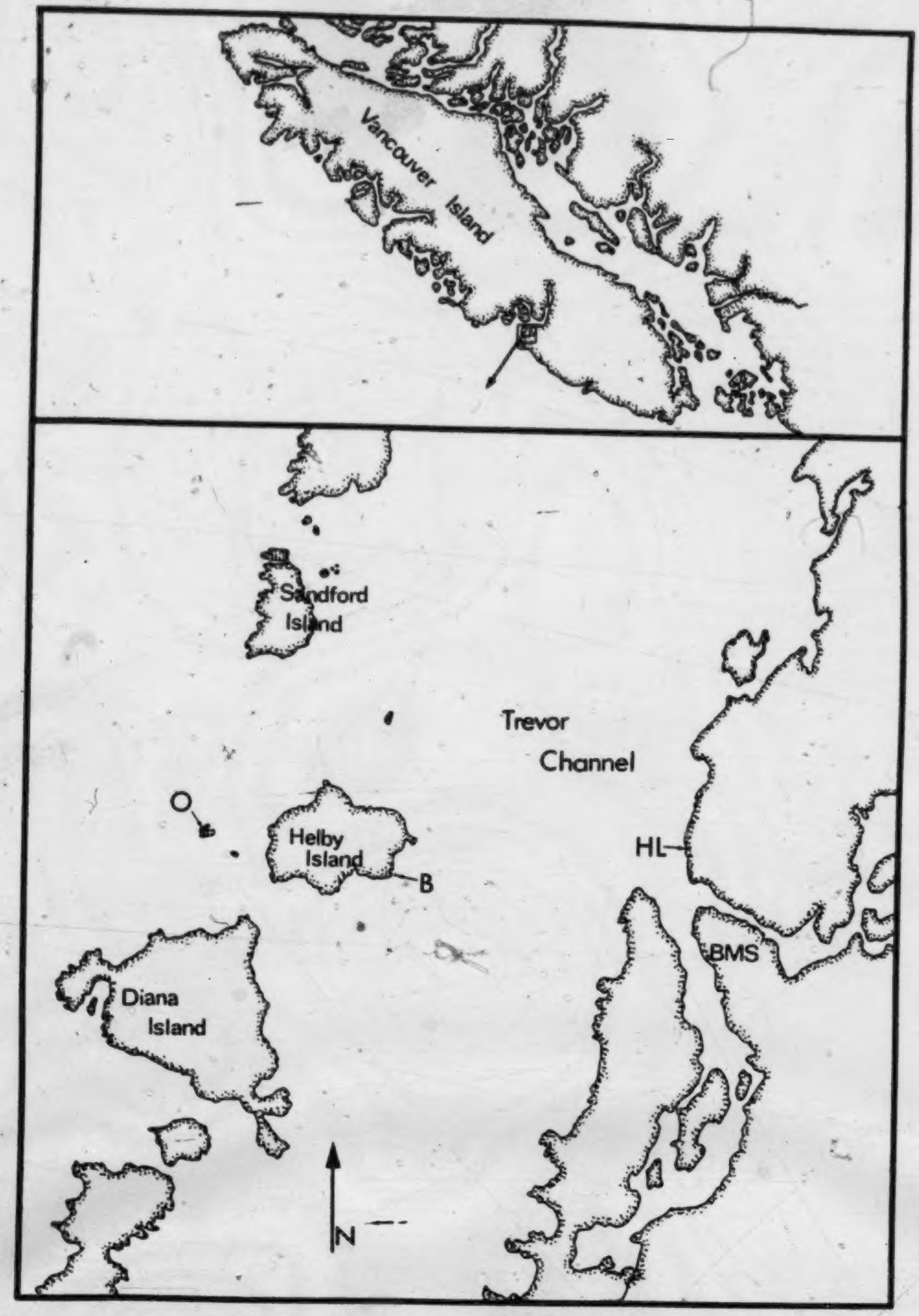
Vancouver Island
Sandford Island
Trevor Channel
O
Helby Island
B
HL
BMS
Diana Island
N

Figure 1. Study areas in Barkley Sound, Vancouver Island. O=Ohiat Islet. B=Blackfish Islet. HL=Harbor Limit. BMS=Bamfield Marine Station.

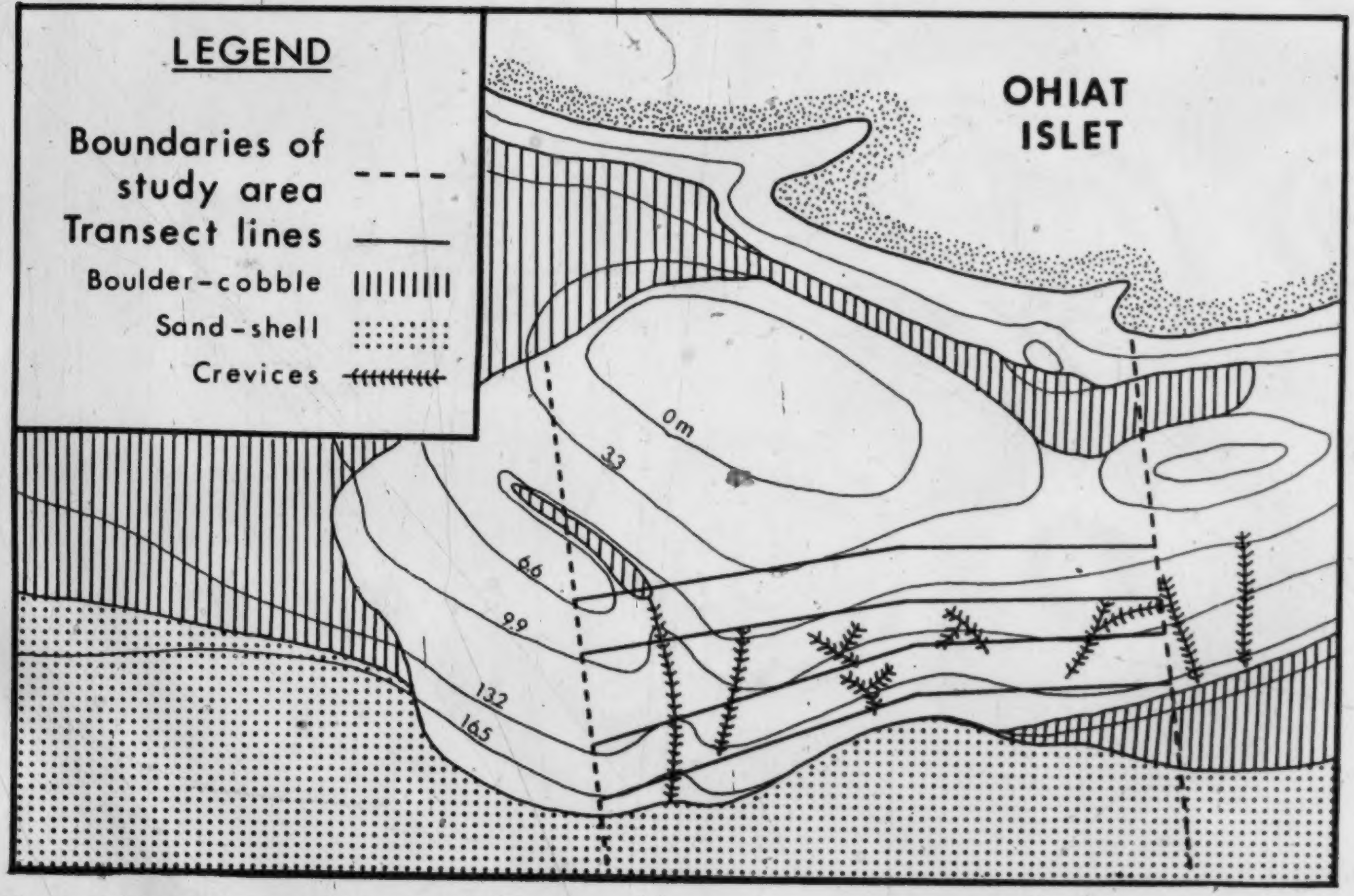
LEGEND
Boundaries of study area - - - -
Transect lines ———
Boulder-cobble ||||||||
Sand-shell ::::::::
Crevices
OHIAT ISLET
0m
33
66
99
132
165

Figure 2. Map of study site at Ohiat Islet showing the boundaries of the study area and transect lines used for estimates of fish density. Solid white areas represent solid rock. Adapted from map by Fletcher (1981).

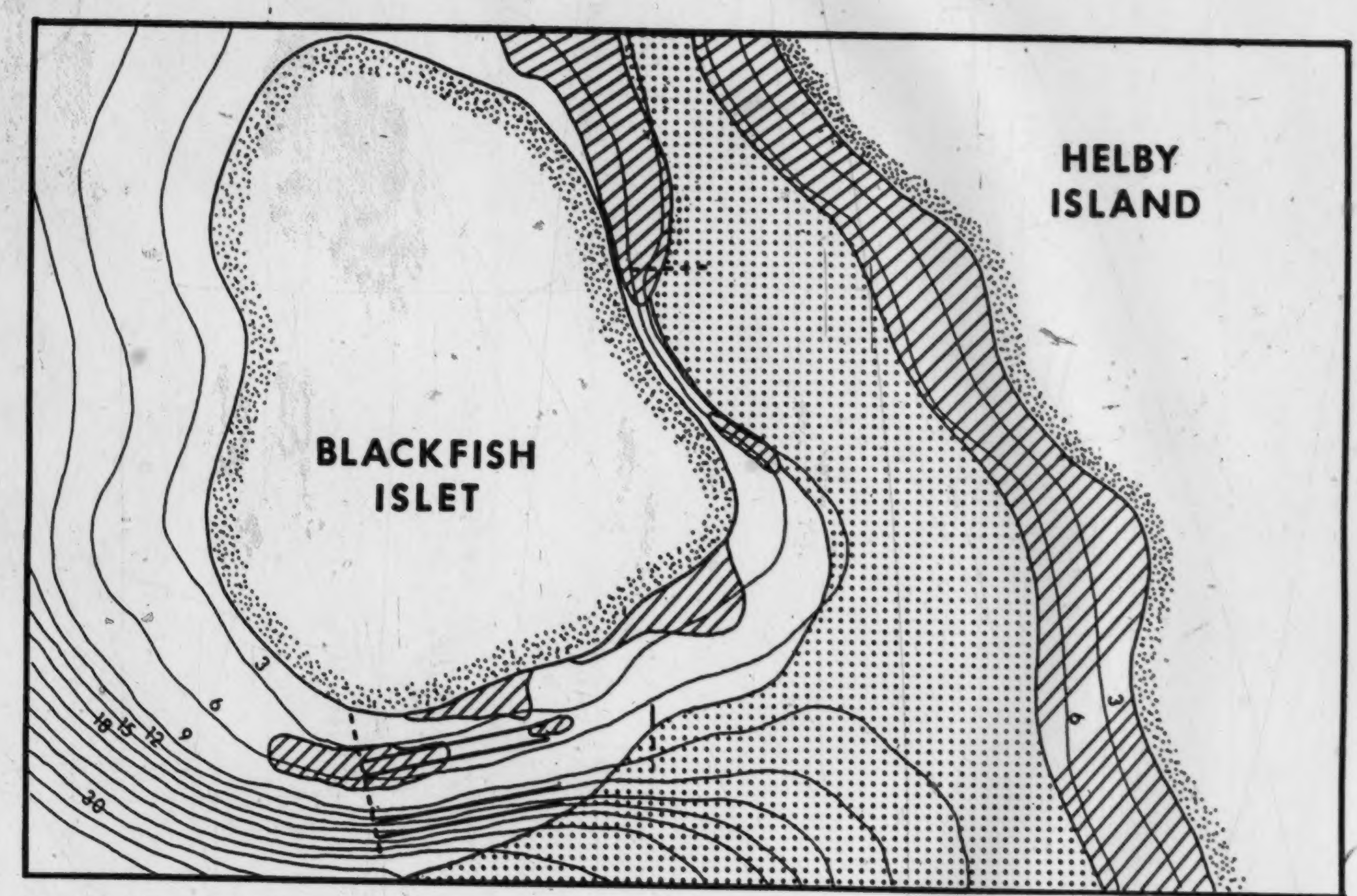
HELBY
ISLAND
BLACKFISH
ISLET
3
6
9
12
15
18
30

Figure 3. Map of study site at Blackfish Islet showing the boundaries of the study area and transect lines used for estimates of fish density. Legend same as for Figure 2.

placed at 1 m intervals on either side of the transect line, and the size (oral disk diameter), orientation (angle from horizontal), site of attachment (crevice or open rock), and depth of each specimen of *Urticina* encountered was recorded on a plastic slate. A numbered plastic tag was then anchored in a crack next to each anemone with a corrosion-resistant nail to aid in future relocation, and serve as a reference point for measurements of anemone movement. The general topography of the area was also recorded. Depths were measured with two oil-filled depth gauges. The measured depths were then adjusted to depths below Canadian chart level by correcting for tidal height at time of sampling. Maps of the transected subtidal area were made so that individual marked anemones could be sampled at regular intervals for associated animals. After 18 months the same areas were resurveyed for newly recruited anemones and tagged individuals were measured for size. Many of the plastic tags were lost throughout the study period, but the location of individual anemones was easily determined in relation to distinguishing topographical features such as crevices or boulders.

Tagged anemones were examined for the presence of associates during both day and night within the same 24-hour period at least once a month. Night observations were done using a high intensity dive light (Super Q-light, Underwater Kinetics) and all observations were recorded on plastic slates or with a small cassette tape recorder placed in a waterproof housing and connected to a microphone in a full SCUBA face mask. A total of 337 *U. lofotensis* and 51 *U. piscivora* were examined during each month's surveys of the 2 study sites. The number, size (total length), sex, activity level, and orientation of the *O. pictus* found with each marked anemone were recorded. Only the number and size of the other fish species associating with the anemones were recorded. Fish were measured in the field at night when they were inactive next to anemones. Most individuals did not respond when a ruler was placed up against the side of their body for length measurements, but a visual estimate of length had to be done for the occasional fish which was disturbed and left its host. Only visual estimates of fish length were possible during daytime observations. When male *O. pictus* were found to be guarding egg masses, the number of spawns was counted and some egg masses were collected. The size and wet weight of the egg masses and the number of eggs per mass were determined as by DeMartini (1976). Some anemones were not examined during the occasional sampling period when either water conditions were too rough in shallow water or the anemones were covered with kelp. These anemones were not considered in the data analysis.

Individual *O. pictus* were identified by their size, sex, behavior, subcutaneous tagging with acrylic dyes (Thresher and Gronell, 1978), or by cutting different dorsal spine combinations (Rinne, 1976). Tagging of *O. pictus* was done underwater at night when fish were quiescent and easily captured in plastic bags. Eleven fish were tagged in the fall of 1984, and seven fish were tagged in the fall of 1985. Four fish appeared to be lost due to the tagging procedure since they were never observed again in the study areas after tagging. Tagged fish were recognized for up to four months.

Population densities of fishes were determined using a variation of the strip count method of Keast and Harker (1977). Two highly visible, yellow 30 m transect lines were placed 3 m apart, parallel to the shoreline in both shallow and deep water (Figures 2 and 3). The ends of the lines were attached to expander bolts set into holes drilled in the rock substratum at the Blackfish and Ohiat Islet sites, and to concrete bricks at the Harbor Limit site. The two shallow transect lines were placed directly above the two deep water lines. At Blackfish and Ohiat Islets the shallow transect lines were at depths of approximately 8-10 m. The deep lines were at approximately 14-18 m. At the Harbor Limit site, the transect lines were placed at depths of 5-7 m and 8-10 m.

The number, approximate size, and sex of *O. pictus* observed within the transect boundaries and 3 m of the bottom were recorded by a diver during a slow swim between the transect lines. The number of *A. harringtoni*, *J. zonope*, and *C. nicholsii* were also counted during surveys at Blackfish and Ohiat Islets. *Oxylebius pictus* population surveys conducted in other areas of Barkley Sound were done by counting the number of *O. pictus* seen within an estimated area covered during an entire dive.

Population surveys were also done for large fishes which are known to feed on the associates of the anemones. Surveys were done at both Blackfish and Ohiat Islets using the above transect methods during monthly day and night examinations of anemones. A high intensity dive light was used during night surveys, and also during the day to inspect holes and crevices for fishes. The diel activities of the fishes were evaluated by noting their behavior and vertical height in the water column (Ebling and Bray, 1976). Fishes were noted as either active or inactive, and their vertical height in the water column was recorded as being in one of four zones (Table 1). The responsiveness of the fishes to the presence of a diver was also used as an indicator of activity (i.e., if the fish swam away or remained unresponsive).

To determine the proportion of the population of *O. pictus* which associated with sea anemones at the study sites, surveys were done of the entire vertical area between the parallel transect lines (Figures 2 and 3). The approximate size and sex were recorded for each fish observed during consecutive 30 m horizontal surveys (approximately 3 m in width) from the deepest to the shallowest parts of the study areas. The number of fish observed during these surveys was compared to the number of fish observed to associate with the anemones at night within the same area. An estimate of the proportions of the populations of the other fish species which associated with anemones was done by comparing densities from transect surveys to that of corresponding examinations of the anemones within the transects.

The number of copepods present on *U. lofotensis* and *U. piscivora* was determined by illuminating the anemones with a high intensity dive light and recording the number of individual *Doridicola* observed on the total area of the oral

Table 1. Zones of vertical orientation in which fish were observed during transect surveys (adapted from Ebling and Bray, 1976)

Zone		Extent of zone
IV	Mid-water	Greater than 1.0 m above the bottom, in open water
III	Suprabenthic	Within 1.0 m of the bottom
II	Bottom	In physical contact with the bottom yet exposed
I	Shelter	In holes, crevices, or under ledges

disk and tentacles of the anemone. The presence of crabs and shrimps with the anemones was also recorded. The size of the crabs was measured, but crabs smaller than 0.5 cm carapace width were difficult to enumerate since they sheltered next to the pedal disk of the anemone, often under a fold of the column. These small crabs were probably underrepresented in the survey results. Counts of the number of crabs out in the open away from anemones and crevices was done to compare the activity of the crabs between day and night. The total number of crabs observed on open rock surfaces within replicate transect plots (30 X 2 m areas) were counted at Blackfish Islet during both day and night on three separate sampling dates.

Interspecies abundance and co-occurrence

Data from the monthly examinations of anemones were analyzed to determine the patterns of interspecies abundance and co-occurrence on the same host anemones. Co-occurrence was measured with the coefficient of interspecific association (C8), which is based on presence-absence data (Hurlbert, 1969). This coefficient ranges from -1 to 1, corresponding to negative and positive patterns of association. Measures of interspecies abundance were only calculated for comparisons of fishes and copepods. Other species combinations were not attempted since few observations involved more than one individual.

Behavioral observations

Direct behavioral observations of individual *O. pictus* and other associates of the anemones were made either by SCUBA or by the use of a submersible video surveillance camera (RCA, TC1005 enclosed in a PVC waterproof housing). Video observations were conducted at Blackfish Islet. The tripod of the video camera was anchored to the substratum, and the camera pointed towards an anemone with a known fish associate. The video camera was connected by cable to a surface monitor and recorder housed on land. Observations were made during the day and twilight without the use of artificial lighting. At night a 12V sealed beam light was used for intermittent observations. This system allowed continuous observation of the fish when near their host anemones without diver presence affecting the fishes' behavior (Hobson, 1972; Chapman et al., 1974; Helfman, 1978). Video recordings were made of some observations, and tapes were later analyzed in the laboratory.

Stomach content analysis of fishes

The feeding habits of *O. pictus*, *A. harringtoni*, and *J. zonope* were determined by collecting the fishes at night next to their host anemones, killing them with MS-222, and dissecting them for stomach content analysis. Fishes were dissected immediately upon return to the laboratory or were kept at 2° C for up to 1.5 days. The stomach contents were examined under a dissecting microscope and the number and size of each item, and the total mass of the contents were recorded. The items were placed into taxonomic groupings, and a visual estimate of the percent composition by volume was done for each group. This estimate was then used in the calculation of percent total mass. The relative importance index (*R.I.*) was calculated for each taxonomic group (George and Hadley, 1979) as an indicator of its dietary importance.

Interspecies interaction experiments

Observations of *O. pictus* revealed that they often fed on small items on the oral disks of anemones. To determine if they were feeding on copepods, small individuals of *O. pictus* (3-5 cm total length) were introduced into aquaria containing specimens of *U. lofotensis* which had many associated *Doridicola sunnivae*. The fish were left in the aquaria for a period of two days, and were either observed directly, with the observer behind a plastic "blind", or the experiment was recorded on video tape. The number of copepods on the anemones was counted before and after fish were introduced into the aquaria. The stomach contents of the fish were analyzed as described above.

To investigate the effect of *O. pictus* predation on populations of copepods, specimens of *U. lofotensis* with associated copepods were put into different treatment cages designed to either exclude small *O. pictus* (<6 cm total length) or allow the fish access to the anemones. Five medium size anemones (8-10 cm oral disk diameter) were placed into paired replicate cages (90 X 60 X 30 cm) made of PVC pipe covered with either fine mesh netting (0.2 X 0.2 cm), coarse mesh (10 X 10 cm), or without mesh. The cages were placed on the substratum at a depth of 8 m at Blackfish Islet and Helby Island. The number of copepods on each anemone was counted at the start of the experiment, and again after one and two months. Cages were periodically inspected for the presence of small post-settlement *O. pictus*, and the fine mesh cages were occasionally cleaned of adherent debris and growths of diatoms.

Host preference experiments

The preference of the associated organisms for certain species of anemones was tested using individuals of the five *Urticina* species, and specimens of *Anthopleura xanthogrammica* and *Metridium senile*. An overall preference experiment was done with single individuals of all 7 species of anemones arranged in a circle (50 cm diameter) within a sea water table (170 X 73 X 22 cm). Trials were done by placing single individuals of either the fish, shrimp, or crab associates into the aquaria with the anemones. Trials were begun in the morning and the locations of the fishes were recorded that evening near midnight. Different individual fish were used for each trial. Locations of the crustaceans were noted at different times of the day over several days. The anemones were all of approximately equal size (7-9 cm oral disk diameter), and were attached to petri dishes. The location of individual anemones within the circle was randomized by moving the anemones to a different area after each trial. Individuals of *U. lofotensis* were not examined for the presence of copepods prior to the start of the experiment.

Preference experiments were also done in the field using the anemones *U. lofotensis*, *U. piscivora*, and *A. xanthogrammica*. Twenty individuals of each species were randomly placed along each of two 30 m transect lines set up at at Helby Island in shallow water (5 m depth). The locations of the anemones were recorded with respect to their position along the transect lines. The number of fishes associating with the anemones was recorded at one and two month intervals.

The fishes, crabs, and shrimps were usually found next to the column and under the tentacles of their host anemones. This subtentacular space provided an enclosed shelter area for associated organisms. To test if the fishes were associating with anemones because of their unique three dimensional shape, different models of anemones were constructed to approximate various types of subtentacular shelter space. One series of models was made using a column of concrete for a base (6 cm in height, 8 cm in diameter), and rubber tubing for tentacles (Plate 1). Another series of models of the same dimensions was made out of rubber (Plate 2). Ten concrete and rubber tubing models were placed out in the subtidal in the same area as the field preference experiments previously described. These models were examined at night for the presence of associated *O. pictus* on 4 separate occasions. Small post-settlement *O. pictus* (<6 cm total length) were also given a choice between *U. lofotensis* and and rubber model anemones in laboratory experiments. Single individuals of *O. pictus* were placed in aquaria containing one model and one anemone, and the location of the fish was recorded at night. Experiments were also done to test if fish which associated with a certain anemone in the field would also associate with a model anemone in place of their real host. Host anemones of *O. pictus* were removed during the day and replaced by either a concrete and rubber tubing anemone, or a rubber model. The models were then checked the same night for the presence of associated fish.

To test if the presence of copepods on *U. lofotensis* had an effect on the host preferences of *O. pictus*, fishes were given a choice between specimens of *U. lofotensis* with copepods, and specimens without copepods. Individual anemones with and without copepods were placed in aquaria (50 X 25 X 25 cm) the day before the start of the experiment, and a small post-settlement *O. pictus* was added the next morning. The experiment was either recorded with a video camera, or monitored by an observer for a 15 minute period at intervals of a few hours during daylight. The location of the fish was also checked at night when the experiment was ended.

Tentacle adhesion experiments

To test if the fishes were able to contact the tentacles of anemones without being stung, individual fishes were anesthetized with MS-222, and placed on the tentacles of anemones. The fishes were considered to be stung if the tentacles adhered to the fishes and if the tentacles contracted at the site of fish contact. Fish were collected in plastic bags at night when they were inactive, then were held in running sea water aquaria in the laboratory until used in experiments. They were transferred between aquaria in plastic bags full of sea water to minimize disturbance of their epidermal mucous coating. Anemones were attached to petri dishes to allow them to be easily moved between different aquaria. Tests were done before each experiment to ensure that the anemones were capable of nematocyst discharge: 1) coverslips coated in an extract of crab tissue were placed on the tentacles, and then checked for the presence of nematocysts using a compound microscope, 2) a finger of the observer was touched against the tentacles and adhesion was considered evidence of nematocyst discharge.

The adhesive force of the anemone's tentacles to the fishes was measured using the method of Lubbock (1980). Fish were first killed with a 5% solution of MS 222 in sea water. A piece of thread was then put through the mouth and out of the gill aperture of the fish, which allowed it to be tethered to a spring gauge. Individual fish were then lowered onto the tentacles of an anemone. After approximately one second of contact, the fish was pulled out of the tentacles while simultaneously recording the maximum force shown on the spring gauge. All removals were done at approximately the same acceleration by pulling the fish out of the tentacles at a constant rate during each trial. A constant acceleration of 9.8 m/s^2 was used in the calculation of all adhesive forces. Each fish was presented up to three times to different tentacles of the same anemone. Only one or two trials were performed with some anemones which retracted their tentacles during initial trials. All four species of associated fishes, and six species of sea anemones were used in the experiments. All fishes, except *O. pictus*, were of approximately the same size (5-7 cm total length), and the anemones were all between 8-12 cm oral disk diameter. Small *O. pictus* (3-6 cm total length) were used in the experiments. Adhesive force trials were also done with individuals of *O. pictus* which had their epidermal mucous coating removed. Fish were killed with MS 222 and their mucous coating wiped away with a paper tissue.

Individuals of *O. pictus* which had been isolated from anemones for a number of days were placed in aquaria with anemones to determine whether they would display any type of acclimation behavior. Fish were placed in aquaria with individuals of *U. lofotensis* which had many associated copepods for the fish to feed on. This experiment was also conducted with fish which had their epidermal mucous coating removed. The fish were anesthetized, their mucus removed, and then placed into an aquarium to revive and become active. Single fish were then placed into aquaria containing the anemones *U. lofotensis* and *U. piscivora*. The subsequent behavior of the fish and the anemones were either observed directly, with the observer behind a plastic "blind", or the experiment was recorded on video tape. The fish were considered acclimated to the anemones when they could come into full contact with the tentacles without being stung and the anemone did not react to the presence of the fish.

To determine the ontogenetic stage at which *O. pictus* acquires the ability to associate with sea anemones, *O. pictus* eggs were collected from the field and the larvae were reared in the laboratory for up to 6 weeks. The eggs and larvae were presented to the tentacles of *U. lofotensis* and *U. piscivora*, and were monitored for tentacle adhesion. The larvae were also placed in aquaria with anemones and observed for any display of acclimation behavior.

Predation experiments

Both laboratory and field experiments were done to determine if: 1) anemones provided effective shelter from predators, 2) anemones provided more effective shelter than rock holes or crevices, and 3) small individuals of *O. pictus* were more vulnerable to predation than large fish. Predators used in laboratory experiments were chosen by their relative abundance in the study habitats and their known feeding habits. Medium size specimens (15-30 cm total length) of the piscivorous fish species *Sebastes caurinus*, *S. maliger*, and *Hemilepidotus hemilepidotus* were used in laboratory experiments. The small octopus, *Octopus rubescens*, was also used. The fishes and octopuses were starved for a period of one to two weeks prior to the start of experiments.

Predation experiments with *Octopus rubescens* were done in aquaria (50 cm X 25 cm X 25 cm) covered with plexiglass lids to prevent the octopuses from escaping. Each aquarium contained a piece of PVC pipe (approximately 15 cm in length X 5 cm in diameter) for the octopuses to shelter in. The specimens of *O. pictus* placed into the aquaria were either of small (3-6 cm total length) or large size (> 10 cm total length). To test if the octopuses could feed on small *O. pictus* which utilized holes and crevices for shelter, pieces of rock were piled in one end of the aquaria to provide shelter for the fish. The experiments were conducted with or without a specimen of *U. lofotensis* in the aquaria.

The experiments with piscivorous fishes were conducted in large circular tanks (1 m diameter X 1 m water depth) which contained one small or large specimen of *O. pictus* with or without a host anemone. Rock shelter was not provided in these experiments since it was assumed that large piscivorous fishes were unable to prey on organisms which were hidden in holes and crevies which were too small for the predators to enter.

All experiments were checked daily for evidence of predation and to observe interactions between the organisms. Experiments were allowed to continue for a period of up to three weeks or until the test specimen of *O. pictus* was eaten. The feeding behavior of the predators on other food items was also examined in the presence and absence of *U. lofotensis* . The large piscivorous fishes were fed other small fish species which did not associate with anemones, and the octopuses were fed small crabs. The survival of *S. acutifrons* against predation of octopuses was noted for those crabs which associated with anemones and those that did not.

Anemone transplant and removal experiments

In late August, 1984, specimens of *U. lofotensis* were transplanted to the Harbor Limit site (where *U. lofotensis* were rare to absent) to test if *O. pictus* would associate with *U. lofotensis* at these sites, and also to test if the presence of this anemone would have any effect on local *O. pictus* population density. Four areas were set up with permanent transect lines (30 m in length) as previously described. The transect areas were surveyed for *O. pictus* to determine mean population densities. Two surveys were done of each transect on separate days. After the initial surveys were completed, two of the transect areas were left as control sites and 30 *U. lofotensis* were transplanted into each of the other two sites. The structural component of the transplanted anemones was not taken into account in the control plots since it was already known that *O. pictus* would not associate with three dimensional models similiar to anemones and since there was abundant structure already present in the habitat. Therefore, it was assumed that the test was for the effect of the presence or absence of anemones (not solely structure) on the population density of *O. pictus*. The specimens of *U. lofotensis* were collected from other areas in Barkley Sound and were transplanted to the study sites by divers. The anemones were placed on flat open rock surfaces along the transect lines and their locations were noted in relation to the marked lengths on the lines. The transplanted anemones in the treatment sites were surveyed at night for the presence of associated *O. pictus* at monthly intervals for five months. Both treatment and control sites were surveyed on three different occasions for *O. pictus* densities approximately one year later (September of 1985).

To determine if individuals of *O. pictus* utilize particular sites because of the presence of anemones, individual *U. lofotensis* which were known to have associated *O. pictus* were removed from the substratum during the day in November of 1985. That same night, the site where the anemone had been removed was surveyed for the presence of the previously associated *O. pictus*. If a fish was not found within a two meter radius of the removal site, it was considered to have been preyed upon or to have migrated to another area. Control anemones which were not removed were also surveyed for the presence of associated fish. Day and night observations were conducted in the same areas after the removals to check for the presence of *O. pictus*.

RESULTS

Population Biology

Anemones

Large populations of *U. lofotensis* and *U. piscivora* were present at Blackfish and Ohiat Islets (Table 2). These anemones were less abundant at more protected sites near Bamfield Inlet. Small individuals (<6 cm) were not as abundant as large individuals in populations of both species at Blackfish and Ohiat Islets (Fig. 4). The sizes of the anemones did not differ between these sites (*U. lofotensis*, t=1.15, P>0.1, df=184, 151; unpaired t-test; *U. piscivora*, U=249, P>0.1, df=30, 19; Mann-Whitney U-test). *Urticina lofotensis* was over six times more abundant than *U. piscivora* in both areas. Both species were most abundant in shallow water at the Blackfish Islet site (Fig. 5). At Ohiat Islet they were rare or absent above 3 m, and were distributed to depths of 18 m. All small *U. piscivora* (<6 cm) were found at the bottom of the rock slope amongst rock boulders. *Urticina lofotensis* was mostly in cracks and crevices (57% of anemones), but most individuals of *U. piscivora* were attached in open rock areas (87% of anemones). Approximately 55% of the individuals of both species were attached on rock surfaces oriented at angles of greater than 45° from horizontal, and 45% on rock surfaces from 0° to 45° from horizontal.

All of the large individuals in the populations were found at the same locations after 18 months; no anemones moved more than a few centimeters. Some small anemones (<4 cm oral disk diameter) were not found after the initial surveys. The loss rates of individuals in this size class were very high for both species of anemones (50 percent), but these individuals made up a small proportion of the total populations for both *U. lofotensis* (2 percent) and *U. piscivora* (6 percent) (Fig. 4). Recruitment rates were also very low for these two species, with only five "new", small *U. lofotensis* being found over 18 months, and one *U. piscivora*. Measurements of oral

Table 2. *Oxylebius pictus*, *Urticina lofotensis*, and *U. piscivora* densities at different study sites. Mean densities from four separate transects. Statistical comparisons among groups are all significantly different (Kruskal-Wallis tests, $P<0.01$). Multiple comparisons between each pair of sites was done using non-parametric method of Zarr (1974). Significant differences between populations ($P<0.05$) indicated by use of different letters.

Sites	Density (mean no. of individuals/100m^2 ± 1 s.d.)		
	Oxylebius pictus	*Urticina lofotensis*	*Urticina piscivora*
Harbor limit	4.6 ± 1.2 A	0.3 ± 0.3 A	1.0 ± 0.3 A
Blackfish Islet	2.3 ± 0.3 B	37.5 ± 21.7 B	5.0 ± 4.6 B
Ohiat Islet	1.7 ± 1.2 BC	38.3 ± 23.5 B	6.6 ± 2.7 B
Aguilar Point	0.5 ± 0.1 C	1.1 ± 0.1 C	6.5 ± 0.8 B

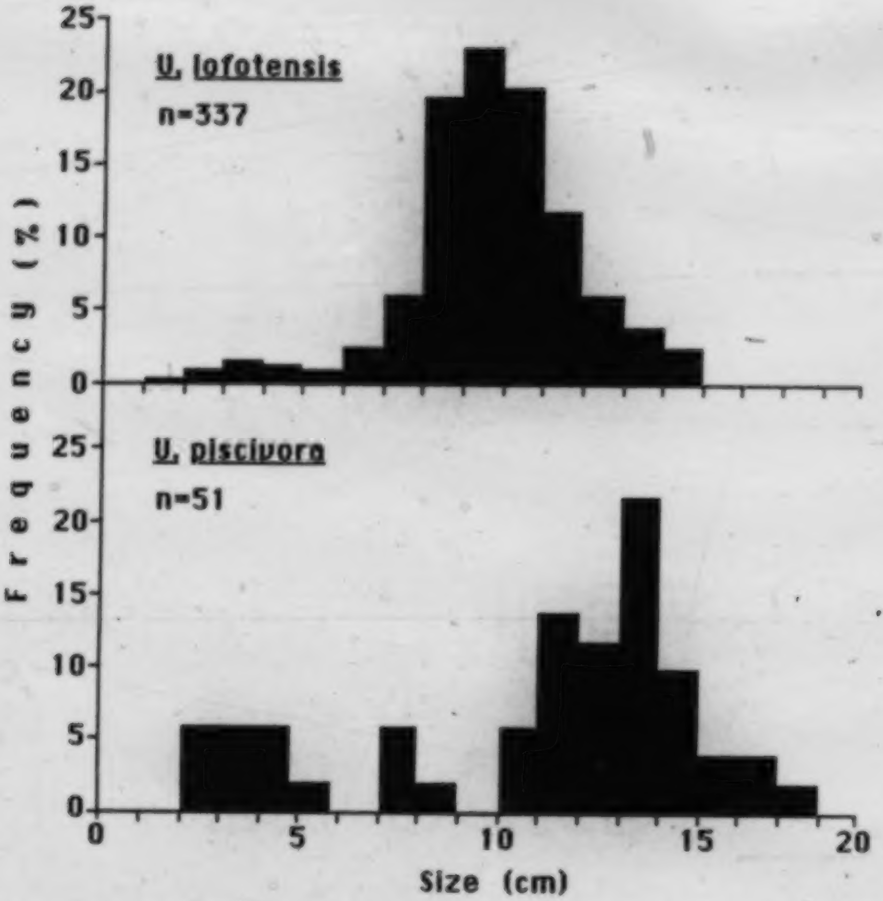

Figure 4. Size frequency distributions of *Urticina lofotensis* and *U. piscivora*. Combined data from both the Blackfish and Ohiat Islet sites.

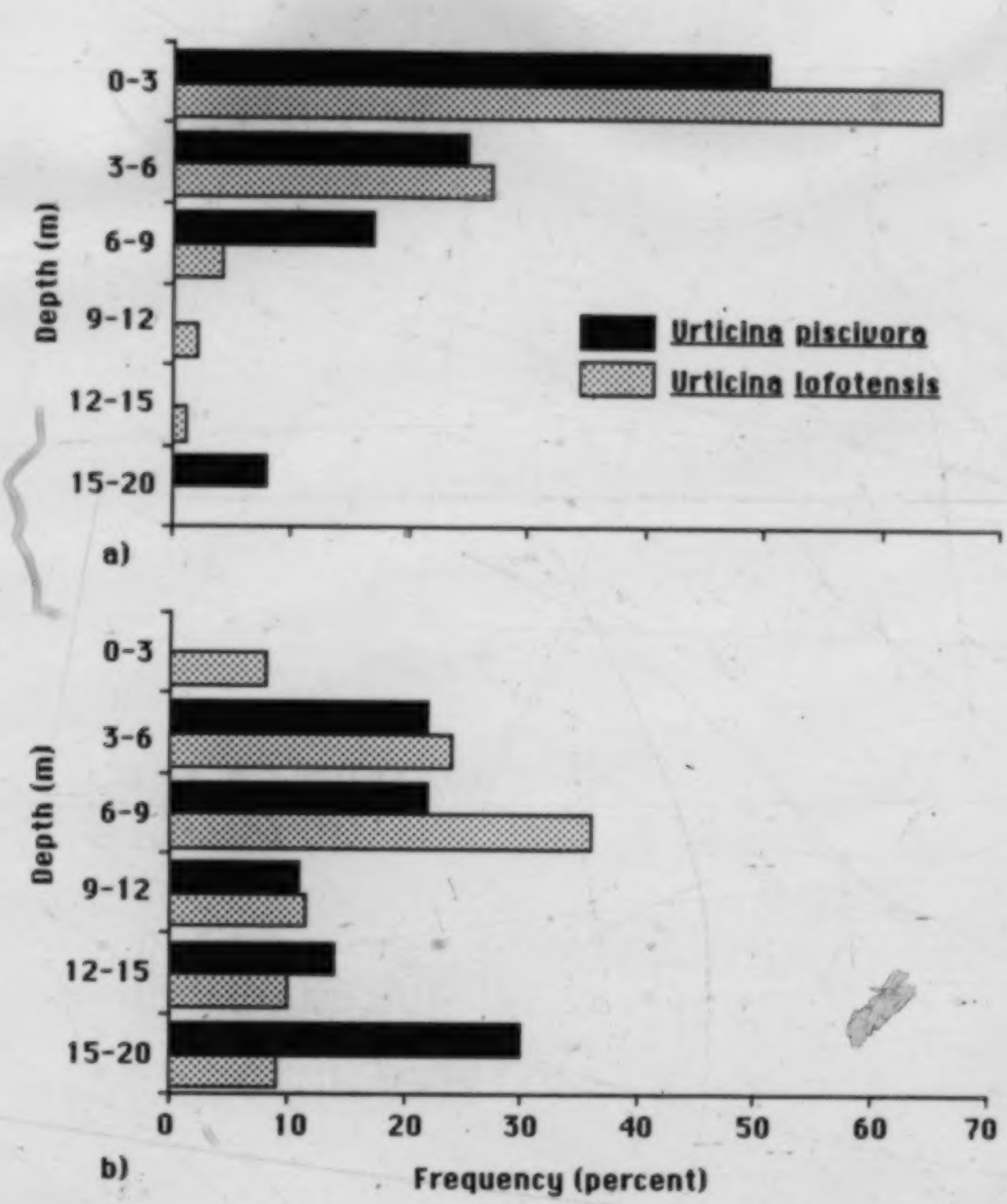

Figure 5. Depth frequency distribution of *Urticina lofotensis* and *Urticina piscivora* at Blackfish (a) and Ohiat (b) Islets.

disk diameter were found to be quite variable over time (1-2 cm between measurements), which precluded any precise measure of growth rates of the anemones over the study period.

Five other species of large sea anemones were also present at the study sites. *Metridium senile* was more abundant than all other species of anemones. It was usually found in aggregations of many individuals, and was present at all depths. Large specimens of the common intertidal anemone *Anthopleura xanthogrammica* were found subtidally in shallow water (<3 m). The three other species of *Urticina* were all rare to absent at the study sites: a total of six *U. coriacea* for both sites, and single individuals of both *U. crassicornis* and *U. columbiana*. *Artedius harringtoni* and *Scyra acutifrons* were often observed with *Metridium senile*, but no fishes, crabs, or shrimps were found associated with the other anemone species. Only qualitative observations were made of these associations, and most effort was concentrated on the associates of *U. lofotensis* and *U. piscivora*.

These seven species of sea anemones differed in the amount of enclosed space beneath their tentacles which an organism was able to use for shelter (Fig. 6). The tentacular crown of some species was high off of the substratum, while others were flush to the substratum, providing no enclosed subtentacular shelter space for associates. *Urticina lofotensis* appeared to provide the most useful shelter space of these anemones, and it also had the largest and most diverse assemblage of associates.

Surveys of *Urticina* anemones at the study sites revealed that most fishes and large crustaceans associated with *U. lofotensis* (>99% of total observations), while very few organisms associated with *U. piscivora* (<1% of total observations). The sample sizes for the number of organisms associating with *U. piscivora* were too small to allow statistical analyses, so these data are only briefly discussed. All

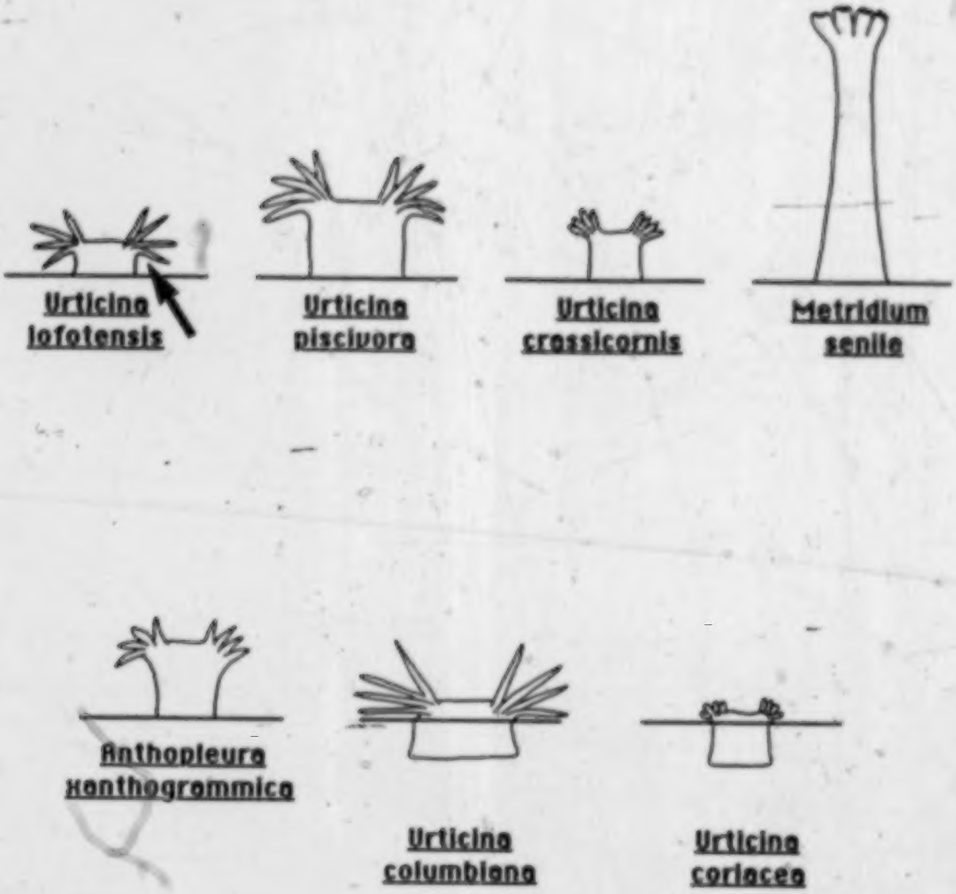
Urticina lofotensis
Urticina piscivora
Urticina crassicornis
Metridium senile
Anthopleura xanthogrammica
Urticina columbiana
Urticina coriacea

Figure 6. Comparison of the subtentacular shelter space provided by different species of large anemones found in the Barkley Sound region. Side view of each species at the level of the substratum. Each diagram approximately one tenth actual size. Arrow indicates the enclosed subtentacular space of *Urticina lofotensis*.

further quantitative results refer to the populations of organisms associating with *U. lofotensis*.

Up to 58 percent of the *U. lofotensis* had associated organisms during a survey, with significantly more anemones having associates at night than during the day (Fig. 7; Table 3). The total number of associates was highest in the fall of 1984, then decreased throughout the winter and did not reach the same peak in the fall of 1985. There was a significant difference between the total number of organisms associating with anemones at Blackfish and Ohiat Islets. There was also a difference between day and night surveys, and months for both sites. More organisms associated with anemones in deeper water at both sites (Fig. 8, Table 4). This was especially evident for the Ohiat Islet populations where the anemones were distributed over a wider depth range. Small *U. lofotensis* (<6 cm oral disk diameter) rarely had any associated organisms (<1% of observations), with most associates being found with the larger anemones in the population.

Oxylebius pictus

Oxylebius pictus population densities were different between the Harbor Limit study site, Blackfish and Ohiat Islets, and Aguilar Point (Table 2). The fish were generally more abundant in calm water areas protected from open oceanic swell, and where the substratum consisted of rocks and boulders. The number of *O. pictus* associating with anemones was not significantly different between Blackfish and Ohiat Islets (Fig. 9, Table 3).

Oxylebius pictus associated most closely with *U. lofotensis* (98% of total observed associations) and rarely with *U. piscivora* (2%). Significantly more *O. pictus* associated with anemones at night than during the day (Fig. 9, Table 3). The fish were active during the day and they were quiescent and relatively unresponsive to the presence of a diver at night. Only small fish (< 6 cm total length) were observed on the oral disks of *U. lofotensis* (Plate 3), but these fish were usually found next to

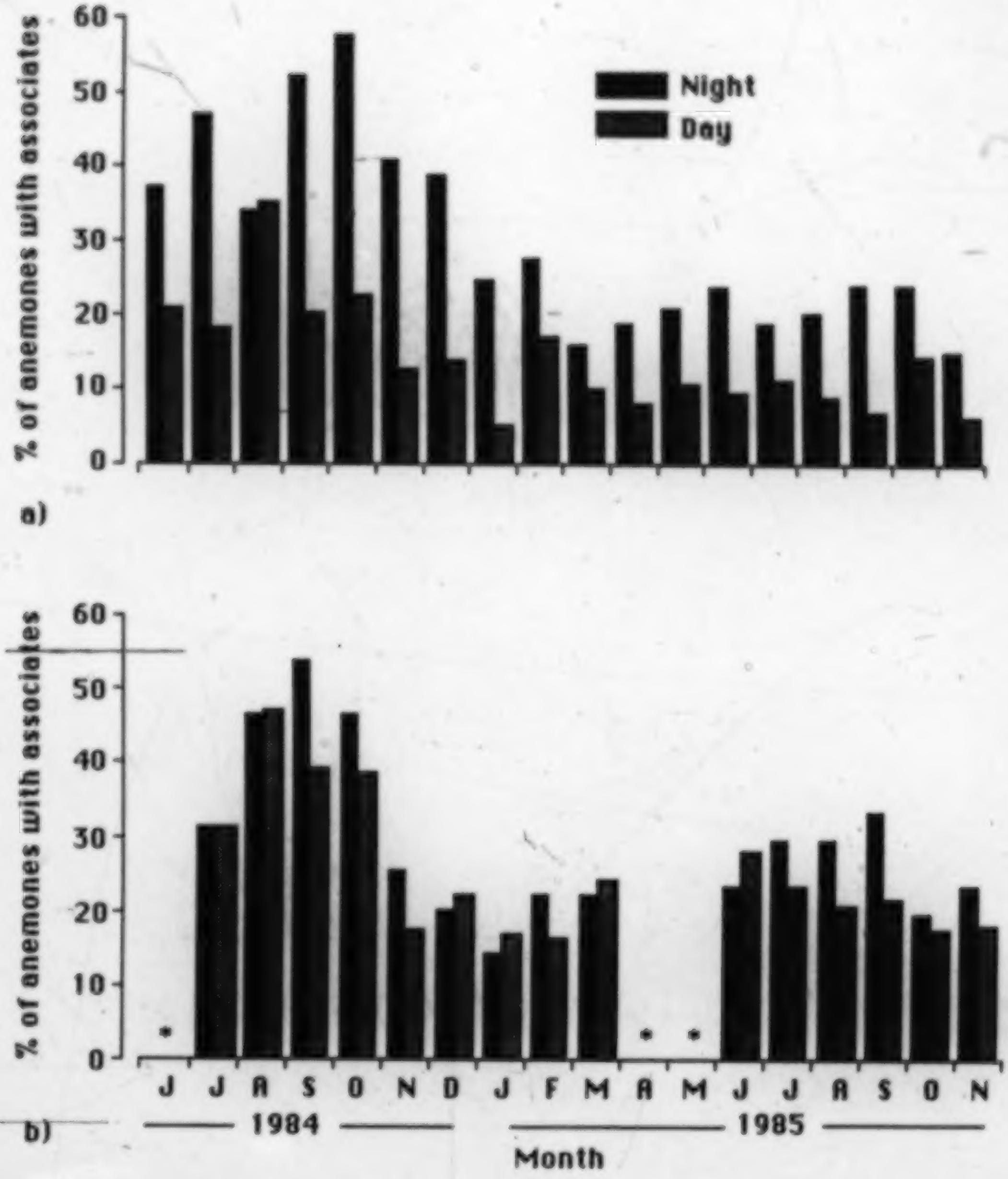

Figure 7. The percent of *Urticina lofotensis* with associated organisms at Blackfish (a) and Ohiat (b) Islets during the day and night. *- indicates no sample for this month.

Table 3. Summary of statistical comparisons of the number of individuals of each species associated with individuals of *Urticina lofotensis* between study locations (Blackfish and Ohiat Islets) (t-tests), day and night (t-tests), and season (months) (Friedman tests). *NC*=not calculated. *P*=probability value. *- total of all associates except *Doridicola sunnivae*.

	Location		Day-night		Season (months)	
	df	*P*	*df*	*P*	*df*	*P*
Total of all species*	175,122	<0.0005	296,296	<0.01	14	<0.005
Oxylebius pictus	175,122	>0.05	296,296	<0.01	14	<0.01
Artedius harringtoni	175,122	<0.05	296,296	<0.001	14	<0.001
Jordania zonope	175,122	<0.01	296,296	<0.001	14	<0.05
Coryphopterus nicholsii	175,122	<0.0001	296,296	<0.001	14	<0.01
Scyra acutifrons	175,122	<0.0005	296,296	<0.001	14	<0.005
Other crabs	175,122	>0.1	296,296	>0.05	14	<0.05
Heptacarpus kincaidi	175,122	<0.05	296,296	<0.2	14	<0.05
Doridicola sunnivae	47,31	>0.25	*NC*	*NC*	13	<0.0001

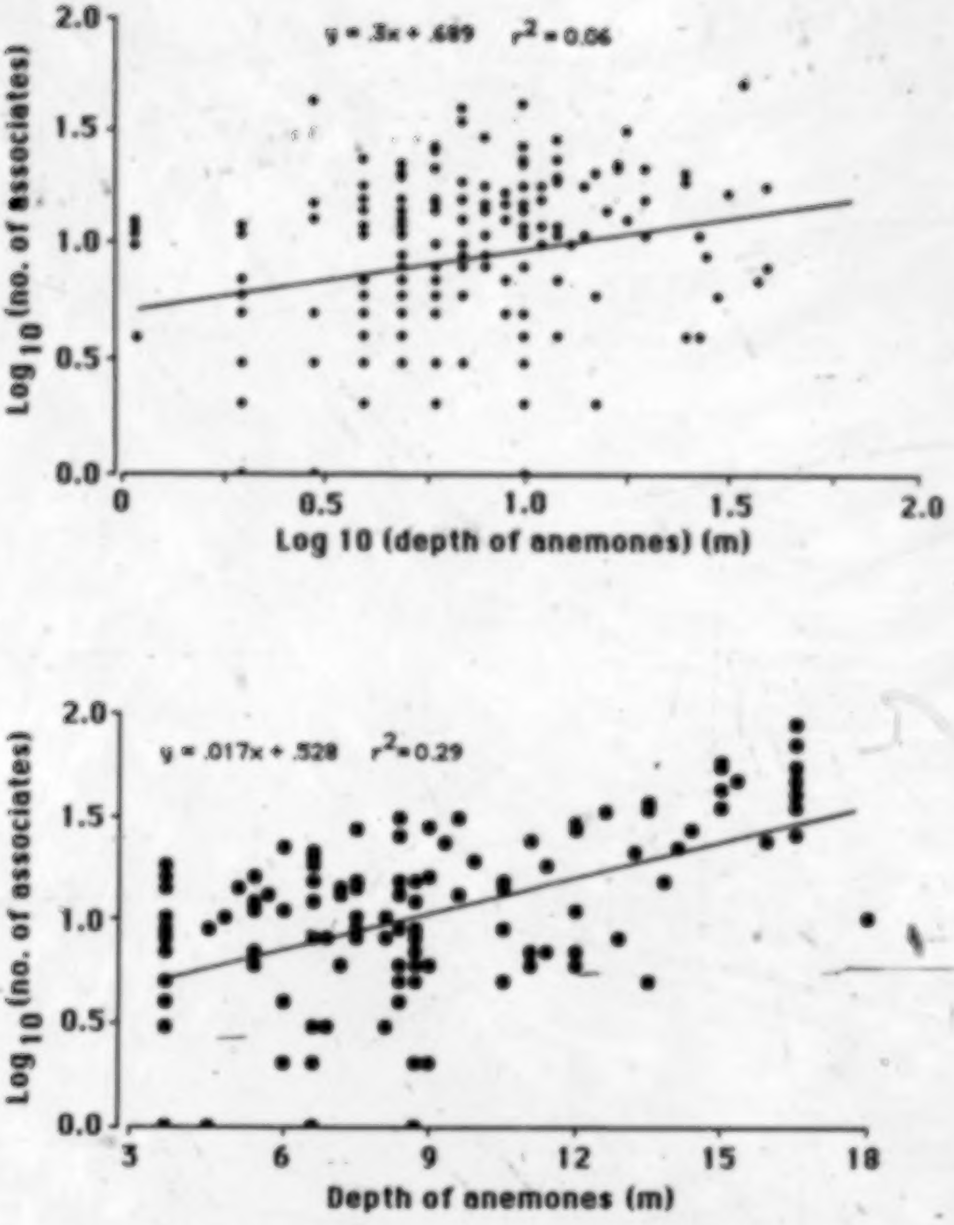

Figure 8. The total number of organisms with individual *Urticina lofotensis* in relation to the depth of the anemones at Blackfish (a) and Ohiat (b) Islets. *- indicates no sample for this month.

Table 4. Summary of statistics for correlations (simple linear regression) between the number of individuals of each species which associated with individuals of *Urticina lofotensis* at different depths. Statistical tests done on totals for each anemone over a period of 15 months, except for *Doridicola sunnivae* in which total number of copepods in samples during May, June, and July of 1985 were used. Refer to Figure 5 for depth distributions of *Urticina lofotensis* at Blackfish and Ohiat Islets. *- total of all species except *Doridicola sunnivae*. **-Spearman Rank correlation coefficient. *NC*=not sufficient data for analysis.

	Ohiat Islet				Blackfish Islet			
	df	r^2	*F*	*P*	*df*	r^2	*F*	*P*
Total of all species*	174	0.29	92.33	<0.0001	121	0.06	9.96	<0.005
Oxylebius pictus	174	0.27	43.62	<0.0001	121	0.00	0.16	>0.25
Artedius harringtoni	174	0.00	0.23	>0.25	121	0.02	3.14	<0.1
Jordania zonope	174	0.03	3.43	<0.1	121	0.02	3.33	<0.1
Coryphopterus nicholsii	174	*NC*	*NC*	*NC*	121	0.01	1.54	<0.25
Scyra acutifrons	174	0.29	48.04	<0.0001	121	0.02	3.98	<0.05
Other crabs	174	0.00	0.03	>0.25	121	0.03	5.79	<0.025
Heptacarpus kincaidi	174	0.44	94.51	<0.0001	121	0.34	90.56	<0.0001
Doridicola sunnivae	**19	-0.64		<0.0001	41	-0.18	8.75	<0.01

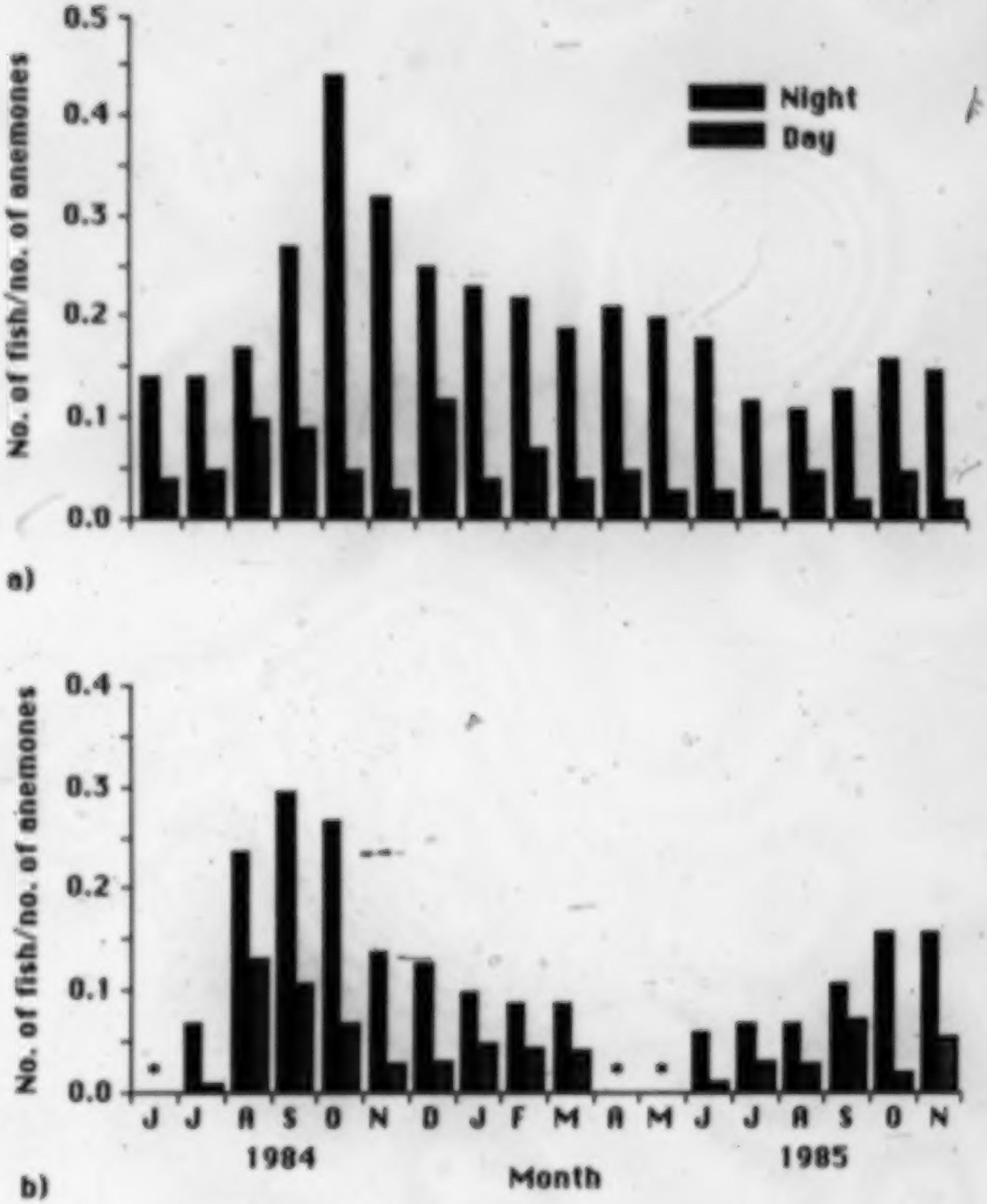

Figure 9. The total number of *Oxylebius pictus* associated with *Urticina lofotensis* / total number of *Urticina lofotensis* at Blackfish (a) and Ohiat (b) Islets. *- indicates no sample for this month.

the columns of anemones (88% of observations for this size class). Large juvenile and adult *O. pictus* were always found under the tentacles next to the column of host anemones (Plate 4). Distinct size classes of *O. pictus* associated most closely with anemones. Juvenile fish (<12 cm total length) accounted for 92 percent of the total number of observations of fish associating with the anemones. Adult males (4% of total number of observations) and females (4%) were rarely observed with anemones.

Surveys of the total area of the study sites within the 30 m transect boundaries showed that juveniles (<12 cm total length) in the populations associated with anemones at night, but few of the adults (>12 cm total length) in the populations associated with anemones (approximately 30 % of individuals). Adult males were highly territorial, and most individuals were consistently found at particular locations within the study areas. They were most common in shallow water at Blackfish Islet (< 8 m), and in deep water at Ohiat Islet (30 m). The fish were usually found in the rock boulder habitats at these depths, except in spring and summer when some males moved to open, solid rock areas to defend spawning territories. Some of the males in the solid rock areas associated with anemones (25% of adult males observed with spawn), and others used holes or rock crevices for shelter.

Males guarded up to three different sets of spawn from late April to August. There was no significant difference in the number or size of egg masses between males which associated with anemones and those that did not, indicating that associated males did not attract significantly more or larger females to spawn (Table 5). Daily examinations of egg masses to detect differences in survival to hatching were not done, but examination of males and their egg masses every few weeks suggested there was no distinct difference in the survival of males or their egg masses between groups, with most fish remaining in the same areas over the spawning period.

Table 5. Comparison of the number and weight of egg masses guarded by male *Oxylebius pictus* which were associated and not associated with anemones. No significant differences between mean number of egg masses between groups (U=40, $p > 0.1$) or wet weight of individual egg masses (U=46, $p > 0.1$). Mann-Whitney U-tests for all comparisons.

	Number of males with egg masses	Number of egg masses per male		Wet weight of individual egg masses (g)
		mean ± s.d.	range	mean ± s.d.
With anemones	7	2.42 ± 2.14	1-6	4.64 ± 1.09 (n=11)
Without anemones	21	1.40 ± 0.51	1-2	3.94 ± 0.95 (n=6)

The number of *O. pictus* associating with sea anemones differed significantly by season (Fig. 9, Table 3). Few small post-settlement fish (< 6 cm total length) were found associating with *U. lofotensis* in July, and their numbers increased throughout the fall (Fig. 10). The number of fish in the populations at all study sites decreased throughout the winter. The fish were active and fed during all months of the year, unlike populations of *O. pictus* in Puget Sound which are inactive during the winter (DeMartini, 1976). Total recruitment of post-settlement fish at Blackfish and Ohiat Islets from July to November of 1984 was estimated as 90 and 81 fish, respectively. By June of 1985 only 30 percent of these fish remained associated with anemones at Blackfish Islet, and 7 percent at Ohiat Islet. There was a large difference in the recruitment of *O. pictus* between the fall of 1984 and 1985. The loss rate of larger fish was much lower than for small post-settlement individuals, but it was not assessed quantitativley since individuals which did not associate with anemones were not always observed during surveys.

Fish smaller than 8 cm total length were less than one year old (Fig. 10). Aging of fish of larger size was attempted by examination of otoliths, but clearing of otoliths with a number of clearing agents was not successful. Fish age was therefore assumed to follow a similar pattern to that described by Demartini (1976) for *O. pictus* populations in Monterey, California, since the size distributions and maximum sizes of the fish were similar for the two areas.

Usually only one fish was found per anemone during the day, but at night more than one fish was often observed with the same host (Table 6). The number of observations of more than one fish associating with the same host anemone increased during the fall when fish population densities were high (Fig. 11). At other times of the year usually only one fish was found per host anemone. Cohabitations were usually between small post-settlement fish, but these individuals were also found to

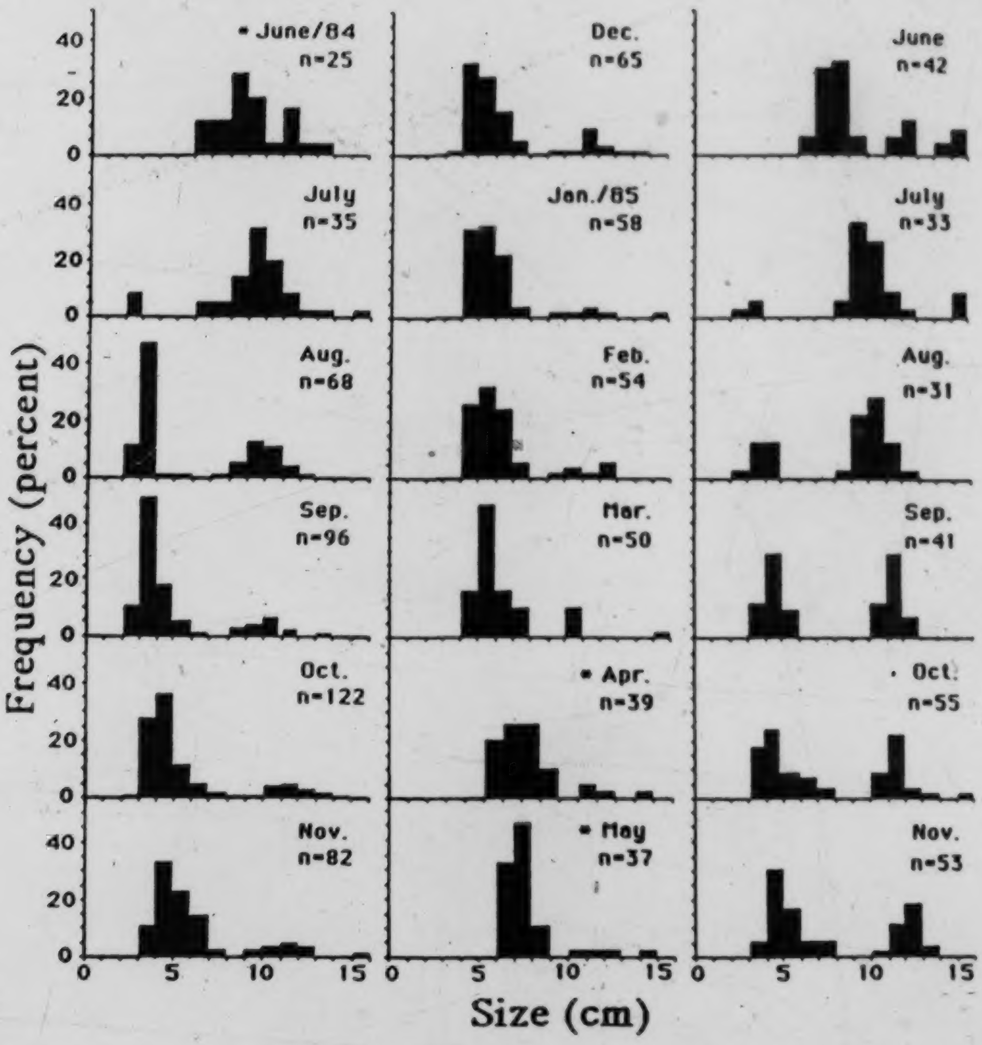

Figure 10. Size distribution of *Oxylebius pictus* associated with *Urticina lofotensis* for each month of the study. Data combined for fish at both Blackfish and Ohiat Islets. *- indicates sample from only Blackfish Islet.

Table 6. Day-night comparisons of the percent of observations of each species with more than one conspecific on the same host. Chi-square tests were conducted on totals of day and night observations over 15 months at both Blackfish and Ohiat Islets. *NC*= no statistic calculated. n.s.= non-significant chi-square statistic.

	% of obs. with >1 individual		*P*	Maximum number of individuals on the same host
	Day	Night		
Oxylebius pictus	5	18	<0.0005	5
Artedius harringtoni	0	9	*NC*	4
Jordania zonope	0	5	*NC*	3
Coryphopterus nicholsii	0	5	*NC*	2
Scyra acutifrons	14	12	n.s.	7
Heptacarpus kincaidi	45	36	n.s.	15

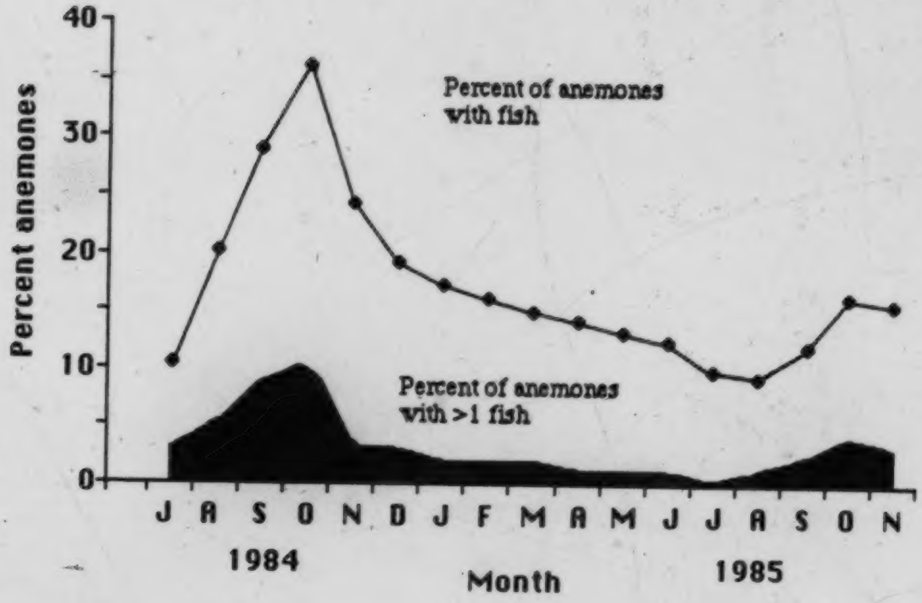

Figure 11. The percent of *Urticina lofotensis* with associated *Oxylebius pictus*, compared to the percent of these anemones with more than one fish.

occur on the same anemones as large juveniles and adults. A maximum of five fish were observed on the same host anemone at night.

Small post-settlement fish rarely associated with *U. piscivora*, but large juvenile and adult *O. pictus* did associate with this species. Two small post-settlement fish were observed next to the columns of two different *U. piscivora*. Four large juveniles (8-12 cm total length), five males, and four females were observed with different anemones. Two of the adult males were guarding egg masses.

More individuals of *O. pictus* were found with anemones on substrata of angles 0^{o} to 45^{o} from horizontal than expected in comparison to the number on substrata of relatively steeper angles ($>45^{o}$ from horizontal) ($P<0.001$, Chi-square test). Anemones on relatively horizontal substrata allowed the fish to rest on the substratum rather than on the column of the anemone. It appeared to be more difficult for individuals of *O. pictus* to remain stable while on the column or oral disk of anemones which were on more vertically oriented substrata. The depth of the host anemone was significantly correlated with the number of associated fish at Ohiat Islet, but not at Blackfish Islet (Table 4). The microhabitat of the host *U. lofotensis* did not affect the association pattern of *O. pictus*, with the same proportions of fish being found with anemones in crevices and in open, solid rock areas ($P>0.1$, Chi-square test).

Tagging studies and continuous surveys of individual anemones indicated that most *O. pictus* associated with the same anemone or groups of anemones within a particular area. In the late summer and early fall, when few small post-settlement fish were present at the study sites, they were easily recognized because of their particular size and the anemone they were found with. Later in the fall when many fish were associating with anemones, tagging of some post-settlement and juvenile fish was done so that individual fish could be recognized. Small post-settlement fish were usually found in the same locations near host anemones during repeated surveys, but large juvenile and adult female fish were not as consistently observed with the same hosts. Some juveniles were found with the same hosts for up to 8 months, and some male fish associated with the same anemone(s) for the duration of the study.

Other associated fishes

Three small benthic fish species (*Artedius harringtoni*, *Jordania zonope*, and *Coryphopterus nicholsii*) were found next to the column of both *U. lofotensis* and *U. piscivora*. All of these fish species were common at the study sites (Table 7), and were often seen sheltering in cracks and crevices away from anemones. These fishes were stung if they contacted their host's tentacles. Fishes were almost always found with *U. lofotensis*, but were rarely observed with *U. piscivora* (<1% of total number of observations). *Artedius harringtoni* was also observed in amongst aggregations of *Metridium senile*. Surveys of the study sites at night and during the day revealed that the fishes were all diurnally active, and that they sheltered in crevices or next to anemones at night (Table 7). More fishes were found with anemones at night than during the day (Table 3).

Artedius harringtoni was the second most common associated fish species; individuals were found with up to 22 % of the *U. lofotensis* at night (Fig. 12). More fish associated with anemones at Ohiat Islet than at Blackfish Islet (Table 3). The population densities of the fish, however, did not differ between these two locations (Table 7). A comparison of the two measures of abundance for the same locations and sampling periods indicated that only a small proportion of the populations associated with anemones at night (approximately 30%). Most fish sheltered in crevices and amongst other sessile invertebrates at night. Fish were most commonly found with anemones during the fall of 1984, but few *A. harringtoni* were observed during the rest of the study period (Fig. 12). This difference in the association pattern between months is significant (Table 3). Fish were found with anemones at all

Table 7. Population densities of fishes (mean number of fish/100m^2 ± s.d.) at the Blackfish and Ohiat study sites. Means are from total number of fish within 2 separate transects at each site sampled during the day and night. Paired t-tests used for comparisons between day and night, and unpaired t-tests for comparisons between sites. *NC*=statistic not calculated.

	Artedius harringtoni	*Jordania zonope*	*Coryphopterus nicholsii*
Blackfish -day	4.2 ± 3.5	1.1 ± 0.8	39.2 ± 0.4
-night	0.8 ± 0.4	0	0.6 ± 0.8
Ohiat -day	4.2 ± 2.0	2.2 ± 2.4	6.4 ± 0.4
-night	1.9 ± 2.0	0	0
P day vs. night	*P*<0.05	*NC*	*P*<0.05
P location	*P*>0.40	*P*>0.1	*P*<0.0001

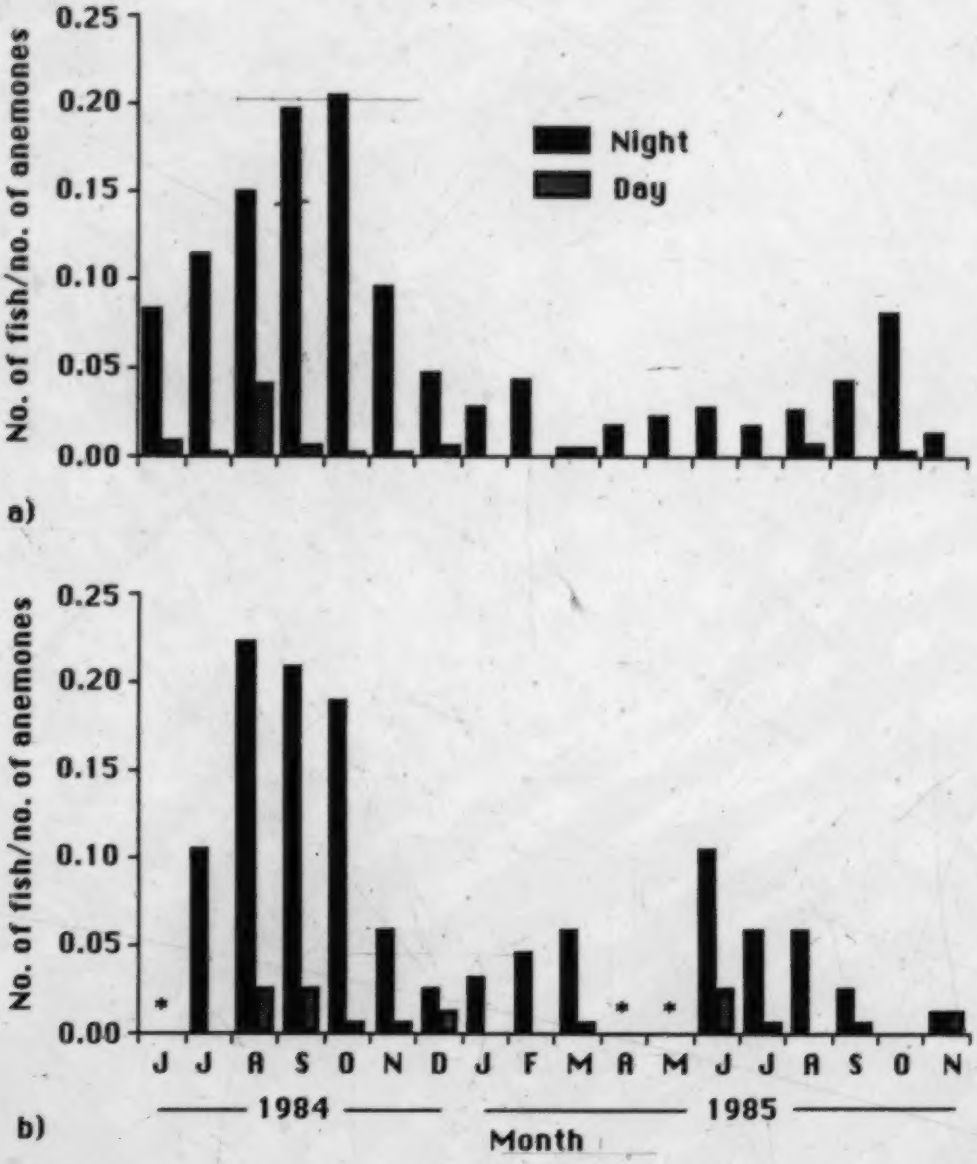

Figure 12. The total number of *Artedius harringtoni* associated with *Urticina lofotensis* / total number of *Urticina lofotensis* at Blackfish (a) and Ohiat (b) Islets. *- indicates no sample for this month.

depths and orientations throughout the study sites. *Artedius harringtoni* was observed in very wave exposed areas throughout Barkley Sound, and it appeared to remain stable on all orientations of substrata. Other species of *Artedius* were also observed at the study sites, but all specimens collected from anemones were *A. harringtoni*.

Individuals of *A. harringtoni* were always solitary with host anemones during the day, but up to 4 fish were found on the same anemone at night (Table 6). The size of the *A. harringtoni* ranged from 3.2-7.8 cm total length (mean=5.0, s.d.=0.4, n=461), which is smaller than the average adult size (pers. obs.) (maximum size=10 cm) (Hart, 1973). There did not appear to be any significant difference in the size distributions of associated fishes between samples.

Jordania zonope and *C. nicholsii* were only observed with anemones during the summer and fall periods of the study (Figures 13 and 14). The seasonal differences in their association patterns were significant (Table 3). *Coryphopterus nicholsii* was more abundant at Blackfish Islet (Table 7), and only two fish were observed with sea anemones at Ohiat Islet. Most of the *C. nicholsii* counted during transects at Ohiat Islet were in the deeper areas of the site. This fish species was usually observed on horizontal surfaces, and it did not rest on vertical rock faces. Significantly more fish associated with anemones on substrata of angles 0° to 45° from horizontal, than on substrata of angles >45° from horizontal (P<0.001, Chi-square test). In contrast, individuals of *J. zonope* were often observed on vertical rock faces, and they associated with anemones on substrata of all orientations.

Only a small proportion of the populations of *J. zonope* and *C. nicholsii* associated with anemones. However, an accurate determination of percentage of the populations was not possible since no fishes were found with anemones at the time of population density surveys (February-March, 1985) (Fig. 7). Associated individuals of *J. zonope* ranged in size from 4.5-10.0 cm total length (mean=6.0, s.d.=1.2,

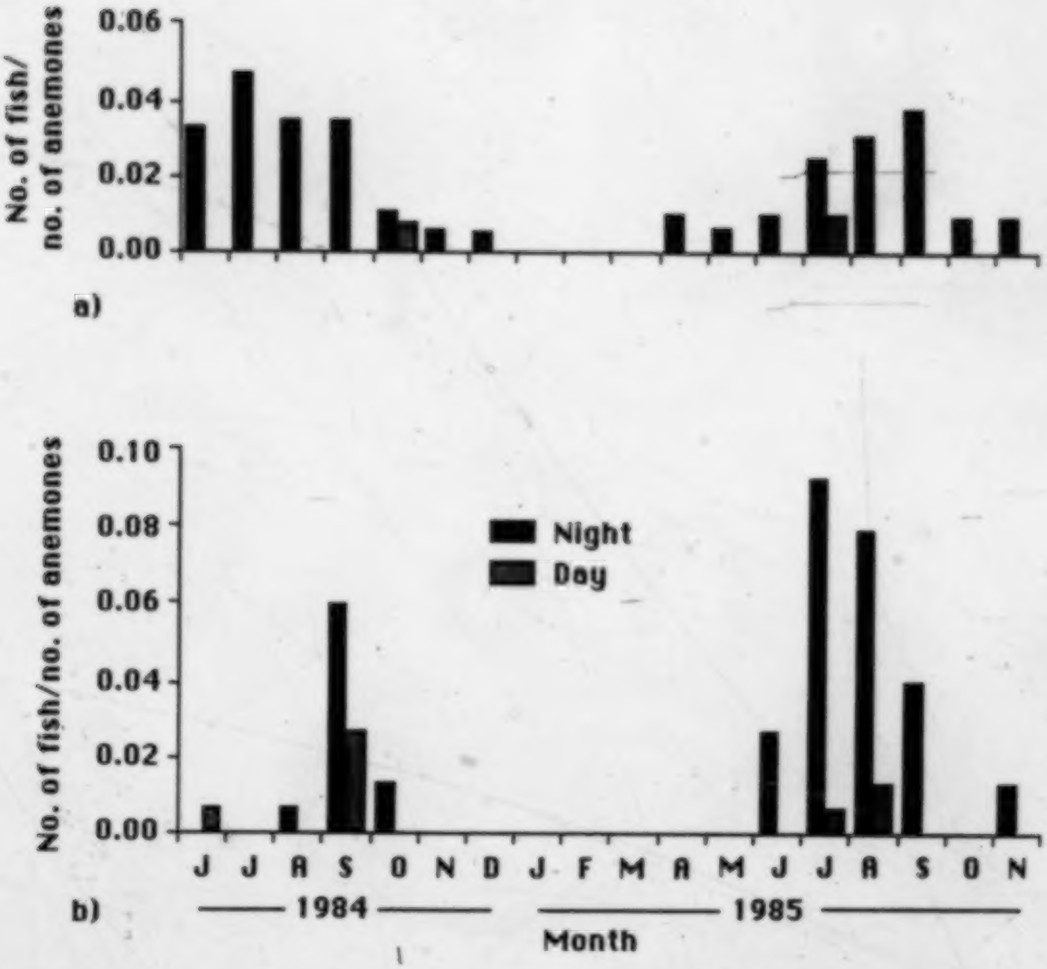

Figure 13. The total number of *Jordania zonope* associated with *Urticina lofotensis* / total number of *Urticina lofotensis* at Blackfish (a) and Ohiat (b) Islets. *- indicates no sample for this month.

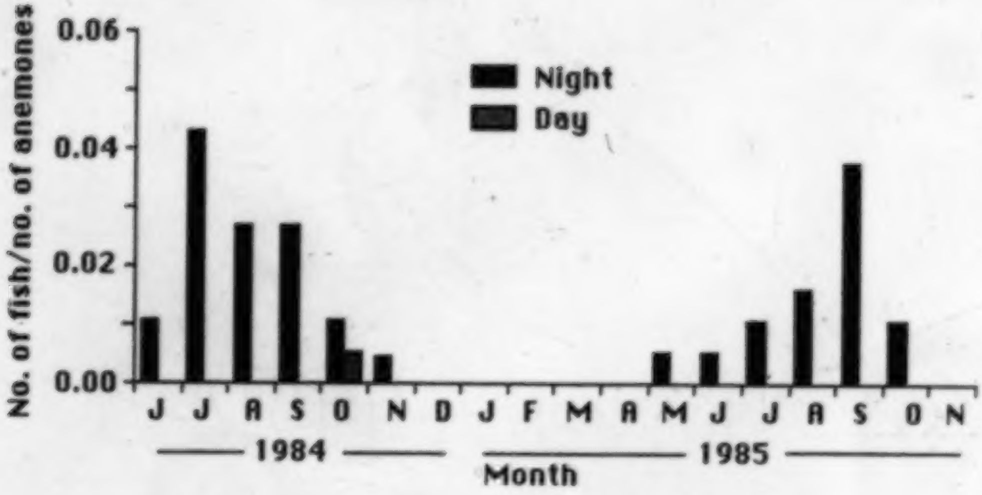

Figure 14. The total number of *Coryphopterus nicholsii* associated with *Urticina lofotensis* / total number of *Urticina lofotensis* at Blackfish Islet. *- indicates no sample for this month.

n=124), and the *C. nicholsii* ranged in size from 5.0-9.5 mm in length (mean=7.5, s.d.=1.1, *n*=39). These fish did not represent any distinct size class of the resident populations. A maximum of one fish was found per host anemone during the day. Most fishes were solitary at night also (Table 6).

Doridicola sunnivae

Examination of *U. piscivora* in the field and in the laboratory revealed the presence of only an occasional copepod associate. However, many *D. sunnivae* were found on the oral disk and tentacles of *U. lofotensis* (Plate 6). Both red and white copepods were present, the latter being more abundant (Fig. 15). Population densities on the anemones did not differ between Blackfish and Ohiat Islets (Table 3). The number of *D. sunnivae* found per individual *U. lofotensis* was highest during the late summer and fall (Fig. 16). Few copepods were present during other times of the year. Seasonal copepod population densities were highly correlated with monthly surface sea water temperatures (Cape Beale lighthouse data, L. Giovando, pers comm.) throughout the study period ($r^2_s=0.90$, $P<0.001$, Spearman-rank correlation). When temperatures rose to a maximum in August, copepod populations also increased to maximum densities. Copepod densities were negatively correlated with the depth of the host anemones at both Ohiat and Blackfish Islets (Fig. 17, Table 4). Water temperatures vary between 2 to 6 degrees celsius between the surface and a depth of 20 m during the late summer and fall in the Bamfield area (Lee and Stucchi, 1983).

Scyra acutifrons and other crabs

Many different crab species were found next to the columns of sea anemones. The most common associate was *Scyra acutifrons* (89% of crab associations), and other crabs were only found occasionally with anemones: *Pugettia richii* (5%), juvenile *Cancer productus* (4%), *Phyllolithodes papillosus* (1%), *Cancer oregonensis* (<1%),

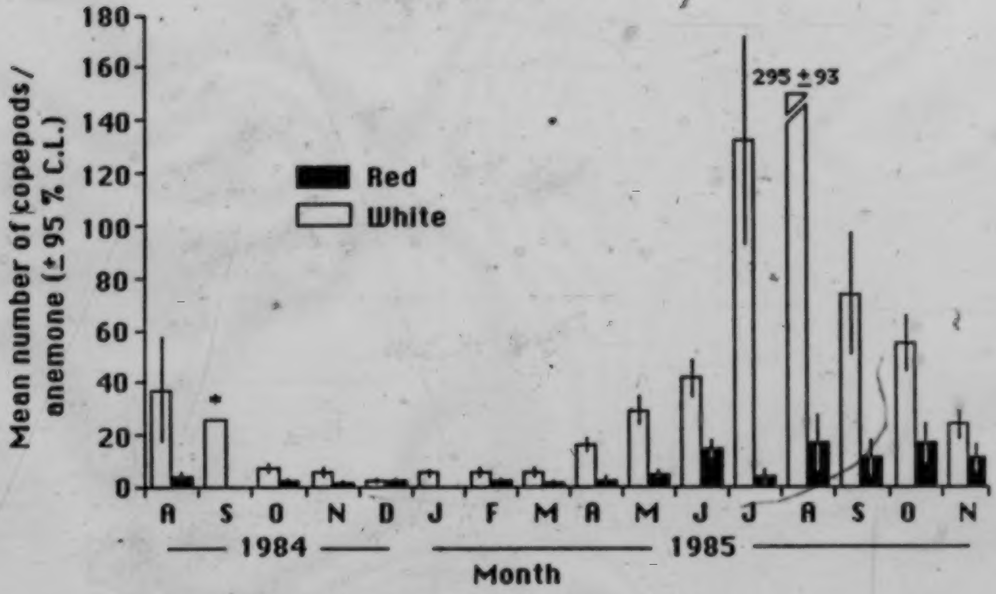

Figure 15. Population densities of red and white *Doridicola sunnivae* on *Urticina lofotensis*. Data for both Blackfish and Ohiat Islets. *- indicates mean for combined total of red and white copepods.

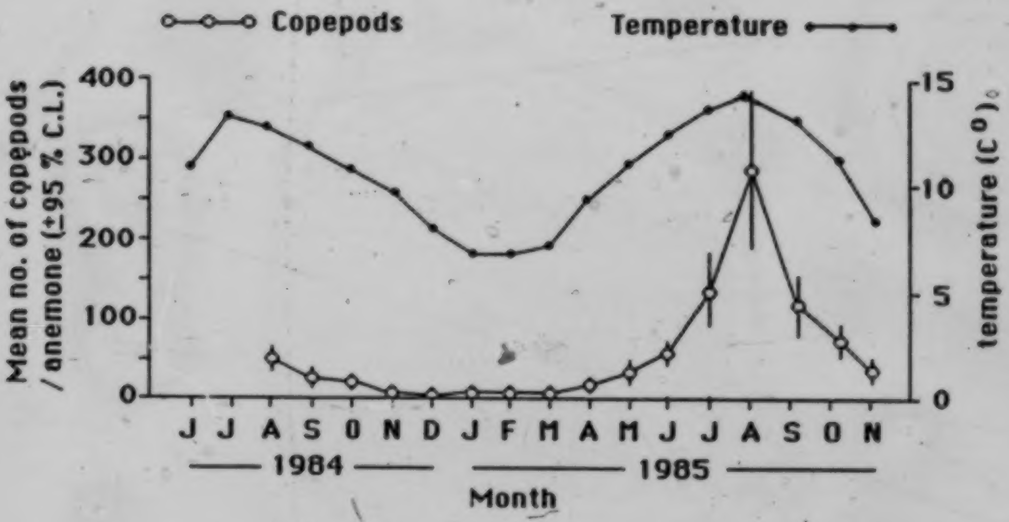

Figure 16. Seasonal population densities of *Doridicola sunnivae* on *Urticina lofotensis* in relation to surface sea water temperatures.

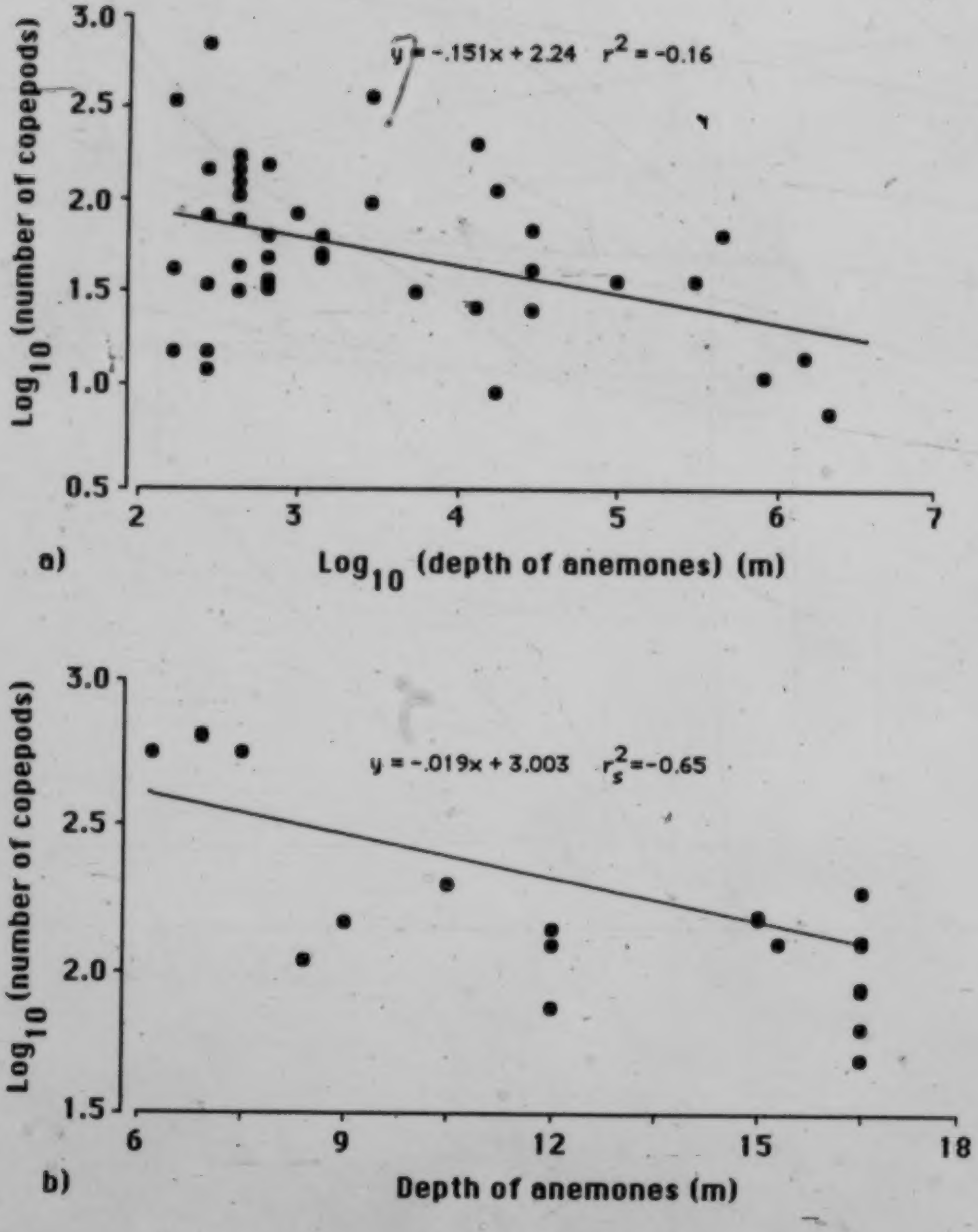

Figure 17. The density of *Doridicola sunnivae* on individual *Urticina lofotensis* in relation to the depth of the anemones at Blackfish (a) and Ohiat (b) Islets. *- indicates no sample for this month.

and *Oregonia gracilis* (<1%). The crabs were usually oriented with their rostral ends facing out from the anemones and their 3rd and 4th pair of walking legs clinging to the anemone's column (Plate 7). All species of crabs came into contact with the tentacles of *U. lofotensis*, apparently without being stung. Large numbers of *S. acutifrons* were observed with *U. lofotensis*, but these crabs were rarely observed with *U. piscivora* (<1% of observations). *Scyra acutifrons* was also found with other species of anemones, especially within aggregations of the anemone *Metridium senile*.

More *S. acutifrons* associated with anemones at Ohiat Islet than at Blackfish Islet (Fig. 18; Table 3). The number of the crabs with anemones also varied by season (Table 3). Only a small percent of the population of *S. acutifrons* associated with anemones, with many crabs sheltering in crevices or amongst other sessile invertebrates. Absolute population densities of the crabs were not determined, so it was not known if absolute density was related to the number of crabs which associated with anemones. More crabs were found with anemones in deeper water (Table 4). Significantly more crabs sheltered next to anemones during the day than during the night (Table 3). *Scyra acutifrons* was more active at night. Transect surveys showed that more crabs were out of shelter at night than during the day ($P<0.05$, $n=3,3$; Mann-Whitney U-test). All sizes of crabs associated with anemones (Fig. 19), but medium size individuals were the most common associates. Small crabs (<0.5 cm) were probably underrepresented in the samples since they were hard to find beneath the folds of the column of *U. lofotensis*. Usually only one crab was found per anemone (Table 6), but up to seven crabs were observed around the column of the same host.

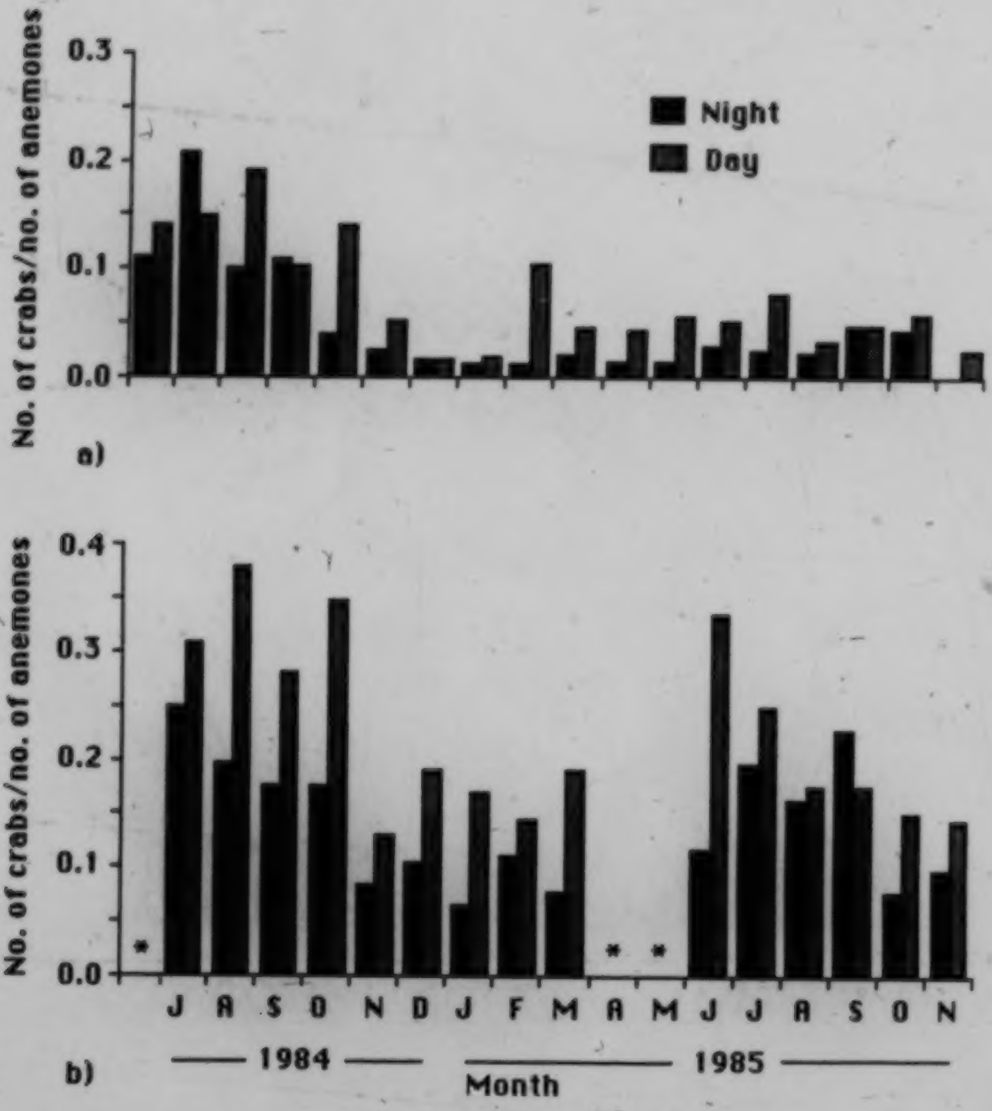

Figure 18. The total number of *Scyra acutifrons* associated with *Urticina lofotensis* / total number of *Urticina lofotensis* at Blackfish (a) and Ohiat (b) Islets. *- indicates no sample for this month.

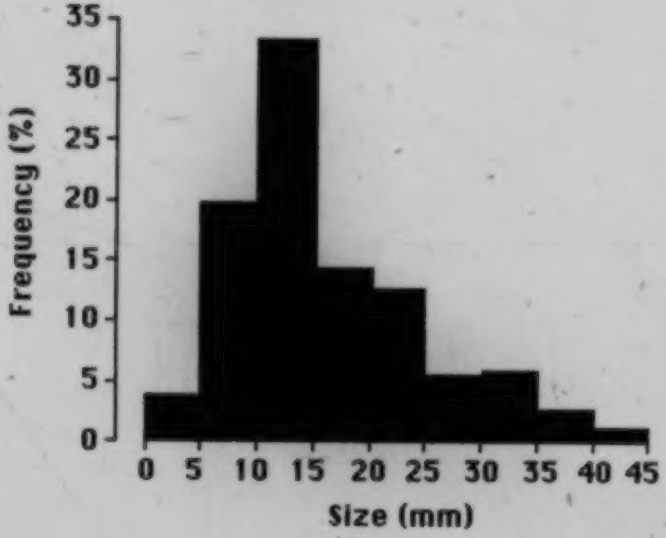

Figure 19. Size distribution of *Scyra acutifrons* associated with *Urticina lofotensis*. Data combined for both Blackfish and Ohiat Islets.

Heptacarpus kincaidi

The number of *H. kincaidi* (Plate 8) associated with anemones varied throughout the study (Fig. 20). Maximum densities were observed in the fall of 1984, then numbers decreased until the fall of 1985. Monthly differences in abundance were significant (Table 3). *Heptacarpus kincaidi* was only observed with *U. lofotensis* in the study areas, but some individuals were also observed with *U. piscivora* outside of the study areas. *Heptacarpus kincaidi* did not appear to be immune to the nematocysts of the anemones, and the shrimp was stung if it came into contact with the tentacles of its host. Shrimps were invariably found with anemones in the deeper areas of the study sites. The number of associated shrimps was correlated with the depth of the anemones (Table 4). The shrimp were hard to observe without the use of a diving light at depths of 15-20 m. Absolute population densities were not determined, but aggregations of *H. kincaidi* were only observed around anemones. More shrimp associated with anemones during the day than during the night, but the difference was not significant (Table 3). Usually more than one shrimp was found per anemone (Table 6), and a maximum of 15 shrimp was observed on one host.

Interspecies interactions

The percent of anemones with either one, two, or three associated species during the day or night is shown in Table 8. These data reveal that only a small proportion of host anemones harbored more than one species of associate at the same time during the day or night. The slightly lower number of species co-occurrences at Blackfish Islet is related to the smaller number of observations of *S. acutifrons* at this site. Analysis of interspecies co-occurrence using Hurlbert's (1969) C8 index resulted in most associations of species pairs being close to 0 (Table 9). This indicates a lack of interdependence in the co-occurrence of these species. Both *Oxylebius pictus* and *Artedius harringtoni* had significant negative associations with *S. acutifrons* during

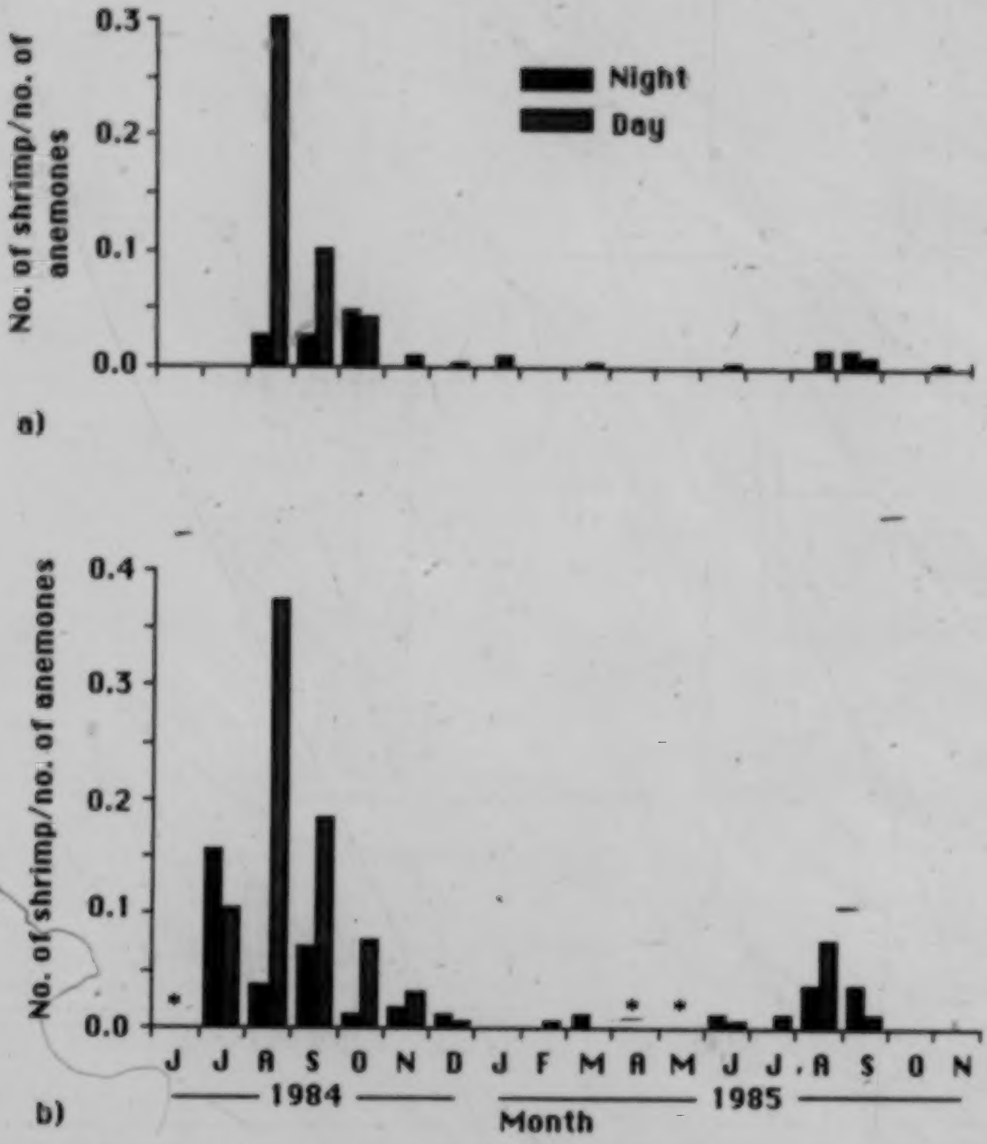

Figure 20. The total number of *Heptacarpus kincaidi* associated with *Urticina lofotensis* / total number of *Urticina lofotensis* at Blackfish (a) and Ohiat (b) Islets. *- indicates no sample for this month.

Table 8. Percent of *Urticina lofotensis* with one, two, or three species co-occurring on the same host. Data from 36 samples of 185 *U. lofotensis* at Blackfish Islet, and 30 samples of 152 *U. lofotensis* at Ohiat Islet.

		Percent of anemones with:			
		0 species	1 species	2 species	3 species
Ohiat Islet	-Day	73	23	3	<1
	-Night	71	24	5	<1
Blackfish Islet	-Day	86	13	<1	<1
	-Night	70	27	3	<1

Table 9. Co-occurence patterns of associated species (C8) as determined from presence-absence data. The C8 statistic is explained in the text. Bottom half of matrix is day C8 values, and top half is night C8 values. *NC*= no co-occurrence. *- indicates significant co-occurrence (Chi-square tests). *=p<0.05, **=p<0.01, ***=p<0.001.

	Oxylebius pictus	*Artedius harringtoni*	*Jordania zonope*	*Coryphopterus nicholsii*	*Scyra acutifrons*	Other crabs	*Heptacarpus kincaidi*
Oxylebius pictus	-	-0.02	* -0.48	*NC*	*** -0.48	-0.69	-0.68
Artedius harringtoni	0.00	-	0.00	*** 0.01	*** -0.45	*NC*	0.00
Jordania zonope	*NC*	0.00	-	0.00	0.01	*NC*	0.00
Coryphopterus nicholsii	*NC*	0.00	*NC*	-	0.00	*NC*	*NC*
Scyra acutifrons	0.01	-0.13	*NC*	*NC*	-	-0.80	*** 0.03
Other crabs	0.23	0.00	*NC*	*NC*	*** -0.21	-	*** 0.05
Heptacarpus kincaidi	0.00	-0.01	*NC*	*NC*	0.02	-0.01	-

night examinations of the anemones. Also, adult *O. pictus* were never observed on the same host as *H. kincaidi* during either day or night samples. The only negative association between fishes was for *O. pictus* and *J. zonope*. These species only co-occurred with anemones which were on horizontal substrata. *Heptacarpus kincaidi* had a positive association with both *S. acutifrons* and the other species of crabs during night samples. During the day, *S. acutifrons* had a negative association with the other species of crabs. There was a significant positive association between the fish *C. nicholsii* and *A. harringtoni* during night samples. Only a few observations of co-occurrence were made of *C. nicholsii* with other species, and these were all at Blackfish Islet.

Behavioral observations

Over 100 hours of observations were made of the behavior of *O. pictus* and host anemones at the Blackfish Islet study site by use of a submersible video camera system. Large juvenile and adult fish were rarely observed near their host anemones during the day (<1% of observation time). Small post-settlement fish (<6 cm total length) spent more time associated with their host anemones than large fish; either next to the column (44% of total observation time for 8 different fish) or on the oral disk of anemones (5 % of total observation time). These fish were observed feeding on the copepods *D. sunnivae* when on the oral disk of *U. lofotensis*. The rest of the time the fish foraged close to their anemones (within 0.5 m radius, 25% of observation time), or were away from their hosts out of the field of view of the camera (26 % of observation time). The host anemones did not appear to change their shape or behavior in response to the presence of *O. pictus* .

Small post-settlement fish returned to their host anemones before dusk and settled next to the column or on the oral disk. Larger juveniles and adults usually returned to anemones during late twilight, and left anemones early in the morning twilight period before light levels were high enough to use the video camera system. Small post-settlement fish remained with their hosts until after dawn. None of the fish exhibited any signs of acclimation behavior to the tentacles of the anemones during field observations, but the tentacles of *U. lofotensis* were occasionally observed to adhere to individuals of *O. pictus*.

Aggressive interactions were observed between fish which cohabited the same host during the day. Larger fish chased smaller fish away from host anemones (n=56 interactions) during the day, but the smaller fish were able to return to the anemones without confrontation during twilight or when larger fish were not present.

No associations between the other fish species and anemones were observed with the video camera system, but some observations were made of large *S. acutifrons*. On 12 occasions during diving and video observation periods large crabs were observed picking at the tentacles of anemones with their chelipeds, or removing food items from the gastrovascular cavity of their hosts. The crabs moved their chelipeds to their mouths and appeared to clean off adherent material with their third maxillipeds. The tentacles of the anemones did not adhere to the crabs, and the anemones occasionally became flaccid during these encounters.

No aggressive interactions were observed between any of the species when they were associated with the same host anemone. However, during the day many agonistic interactions were observed between small post-settlement *O. pictus* and other associated fish species. *Coryphopterus nicholsii* often attacked small individuals of *O. pictus* which entered the goby's territory. *Artedius harringtoni* and *J. zonope* were also observed attacking small *O. pictus*. The *O. pictus* would usually retreat back to its host anemone in response to such attacks, and the other fish would not attempt to follow. Adult *O. pictus* were seen to feed on items around the bases of anemones (where there were usually small crabs), but identification of the prey items was not possible.

Many rockfish species and kelp greenlings (*Hexagrammos decagrammus*) approached individuals of *O. pictus* next to their host anemones. Small post-settlement fish responded to these piscivorous fishes by retreating under the tentacles of their host anemones. Large *O. pictus* either remained stationary or swam away to shelter in rock crevices.

Stomach content analysis of fishes

Stomach content analysis of *O. pictus* confirmed that the fish were preying on *D. sunnivae*. Small post-settlement fish collected at night had a large of number of copepods in their stomachs (Table 10). Most of these were benthic harpacticoid copepods, but many *D. sunnivae* were also present. Copepods were the most important prey items of these small fish, as indicated by their high relative importance index values. In contrast, copepods were a minor item in the diets of large juvenile and adult fish which preyed on mostly gammarid amphipods, caprellid amphipods, and crabs. The presence of hydroids in the stomachs of the fish was probably a result of the fish feeding on caprellid amphipods which were abundant on hydroid colonies. The crabs enumerated were mostly porcellanids, which were not found associated with anemones. No *Scyra acutifrons* or other species of crabs which were observed to associate with sea anemones were found in the samples. The stomach of one large *O. pictus* (11 cm total length), however, contained a *Heptacarpus kincaidi*, a species which was commonly observed with *U. lofotenisis*.

Artedius harringtoni and *J. zonope* also fed on crustaceans (>70% of *R. I.* index) (Tables 11 and 12). Amphipods were important in the diets of both species, but they differed in the types and relative amounts of other items eaten. Crabs and fish were eaten by *A. harringtoni* but not *J. zonope*. Both species fed on harpacticoid copepods, but they made up a larger proportion of the diet of *J. zonope*. Smaller

Table 10. Stomach contents of small post-settlement *Oxylebius pictus*=S (< 6 cm total length, *n*=18 fish) and large *Oxylebius pictus*=L (6-16 cm total length, *n*=14 fish). *R.I.* index refers to Relative Importance Index of George and Hadley (1979).

	Percent of fish		Number of items		Percent of total		Percent weight		*R. I.* Index (percent)	
	S	L	S	L	S	L	S	L	S	L
Harpacticoid copepods	94	28	1019	7	62	3	42	<1	38	5
Doridicola sunnivae	78	36	527	17	32	8	25	<1	26	6
Gammarid amphipods	44	71	42	57	3	26	13	12	11	16
Caprellid amphipods	17	57	14	59	1	27	7	15	5	14
Crabs	0	43	0	13	0	6	0	31	0	12
Megalops larvae	33	50	9	15	<1	7	5	5	7	9
Shrimp	0	7	0	1	0	<1	0	<1	0	1
Isopods	17	36	24	8	1	4	5	<1	4	6
Barnacle cyprids	22	14	5	4	<1	2	1	<1	4	2
Ostracods	6	14	1	3	<1	1	<1	<1	1	2
Unid. crustacean parts	17	86	3	12	<1	5	1	33	4	18
Hydroid parts	0	36	0	22	0	10	0	2	0	7
Foraminiferans	0	14	0	3	0	<1	0	<1	0	2

Table 11. Stomach contents of *Artedius harringtoni* (mean size=5.9 cm, s.d.=1.5, range=2.8-8.8 cm, *n*=18 fish). *R.I.* index refers to Relative Importance Index of George and Hadley (1979).

	Percent of fish	Number of items	Percent of total	Percent weight	*R. I.* Index (percent)
Gammarid amphipods	56	77	34	14	24
Caprellid amphipods	11	5	2	<1	3
Crabs	33	9	4	43	19
Shrimp	6	1	<1	14	5
Isopods	6	2	1	<1	2
Crustacean parts	50	99	43	5	23
Hydroids	39	30	13	4	13
Fish	17	4	2	17	8
Mollusca	6	1	<1	1	2
Unidentified material	6	1	<1	1	2

Table 12. Stomach contents of *Jordania zonope* (mean size=6.2 cm, s.d.=1.9, range=4.7-10.2 cm, *n*=6 fish). *R.I.* index refers to Relative Importance Index of George and Hadley (1979).

	Percent of fish	Number of items	Percent of total	Percent weight	*R. I.* Index (percent)
Gammarid amphipods	50	17	8	16	11
Caprellid amphipods	100	14	8	12	17
Copepods	83	47	23	3	16
Isopods	17	5	2	<1	3
Unid. crustacean parts	100	98	48	23	25
Hydroids	33	4	2	1	5
Nematodes	17	2	1	<1	3
Bryozoans	17	5	2	<1	3
Unidentified material	67	13	6	42	17

fishes of both species were observed to have more copepods in their stomachs than large individuals. None of the copepods found were *D. sunnivae*.

Effect of *Oxylebius pictus* predation on *Doridicola sunnivae*

Small post-settlement *O. pictus* had an effect on the population densities of *D. sunnivae*. During the late summer and fall when larval *O. pictus* settled out of the plankton and began to associate with *U. lofotensis*, the number of copepods per anemone also decreased (Fig. 21). There were significant differences in the number of copepods on anemones with associated post-settlement fish compared to anemones without fish for the late summer and fall months, but not during the winter (Fig. 22). The number of copepods on individual anemones before and after the settlement of a fish was also significantly different (n=29, P<0.0001, Wilcoxon sign-rank). When copepod numbers were increasing during July, however, the density of copepods on most anemones continued to increase despite the presence of an associated fish.

Copepod predation experiments

Post-settlement *O. pictus* were observed feeding on *D. sunnivae* during laboratory experiments. The fish fed on the copepods during extended periods in the tentacles and on the oral disk of *U. lofotensis*. Stomach content analysis of these fish confirmed that they were feeding on the copepods. Over a period of two days a fish was able to remove almost all of the copepods from an anemone. The copepods appeared to respond to predation by the fish by aggregating on the tips of the anemone's tentacles.

Field cages, designed to either exclude small post-settlement *O. pictus*, or allow them access to anemones with associated *D. sunnivae*, resulted in significant differences between densities of copepods on anemones in fine mesh cages and those open to fish (Fig. 23, Table 13). Small post-settlement *O. pictus* were observed on

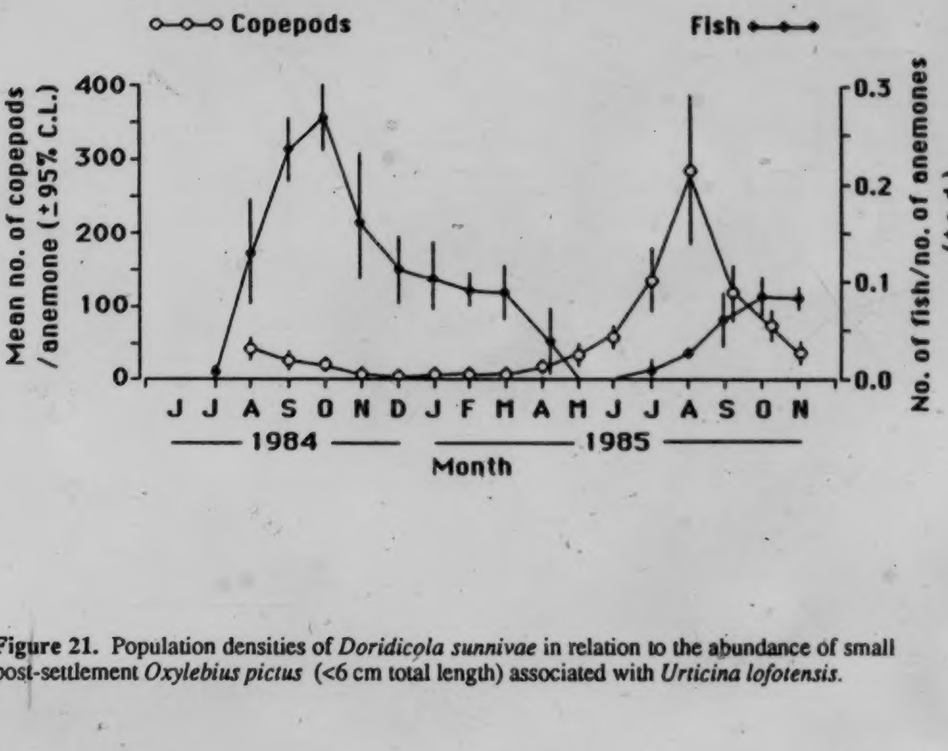

Figure 21. Population densities of *Doridicola sunnivae* in relation to the abundance of small post-settlement *Oxylebius pictus* (<6 cm total length) associated with *Urticina lofotensis*.

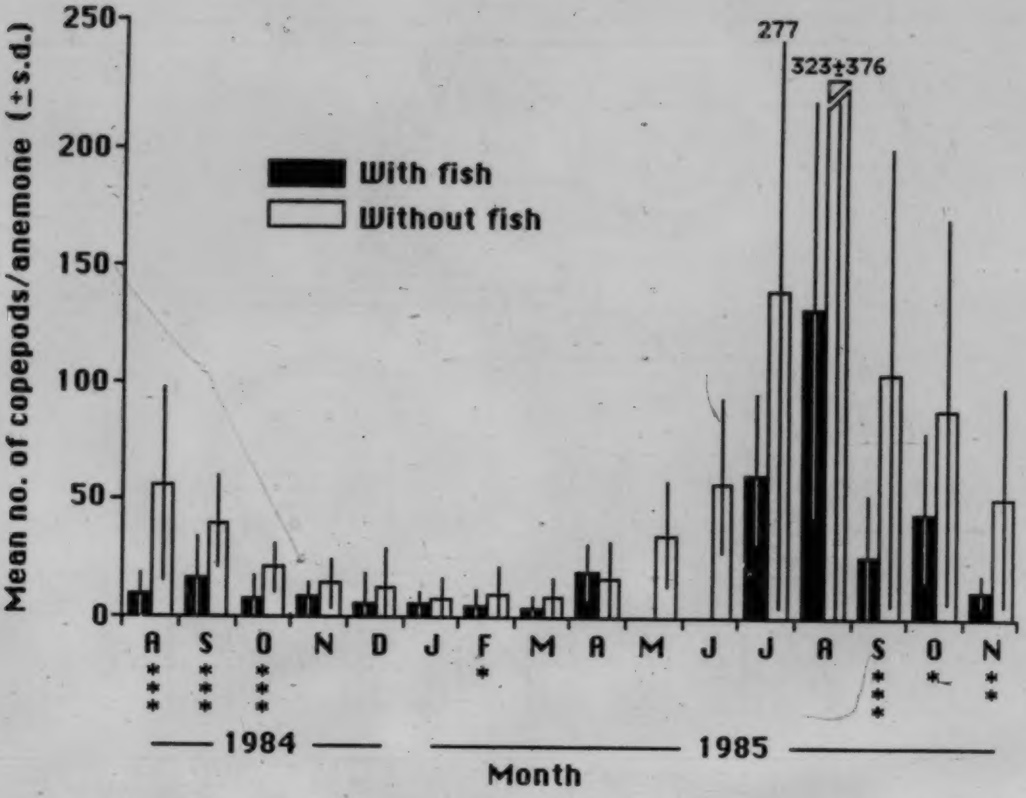

Figure 22. Population densities of *Doridicola sunnivae* on *Urticina lofotensis* with and without associated small post-settlement Oxylebius pictus (<6 cm total length). *-indicates a significance difference between groups for each month. Mann-Whitney U-tests for all comparisons. *=<0.05, **=<0.01, ***=<0.001.

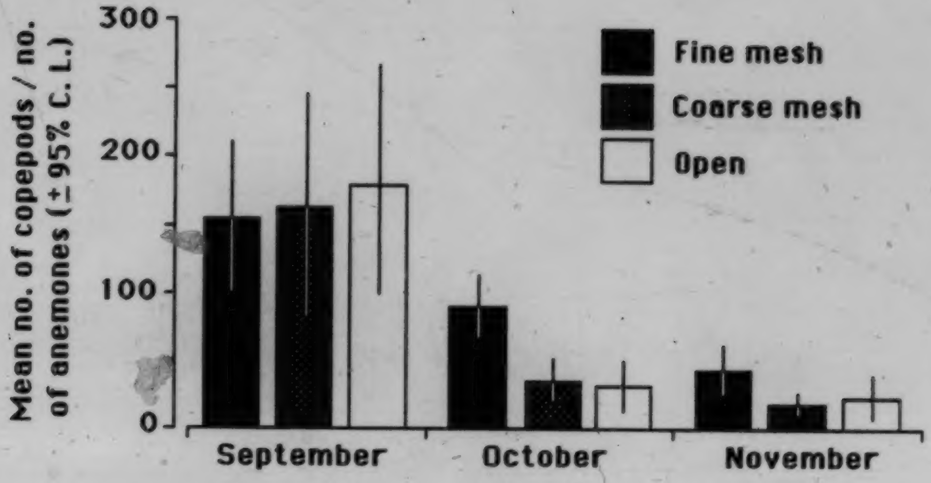

Figure 23. Population densities of *Doridicola sunnivae* on *Urticina lofotensis* in different treatment cages from the start of the experiment in September to one and two months later. Significance tests in Table 13.

Table 13. Statistical analysis of caging experiment shown in Figure 23. Kruskal-Wallis tests for comparisons of densities of *Doridicola sunnivae* on *Urticina lofotensis* in fine mesh, coarse mesh, and open cages at Blackfish Islet and Helby Island at start of experiment in September, and two months afterwards.

Months	*df*	H	*P*
September	2	0.70	>0.7
October	2	12.57	<0.01
November	2	6.34	<0.05

the anemones in the coarse mesh and open cages, but no fish were seen in the fine mesh cages. At the start of the experiment in September, the anemones in each treatment had approximately the same densities of copepods. After one and two months, the copepod densities in all treatments decreased significantly ($P<0.01$, Friedman tests for each treatment).

Host preference experiments

Preference experiments done in the laboratory with six species of sea anemones resulted in only small post-settlement *O. pictus* showing any regular association behavior. Large *O. pictus* and the other fish, crab, and shrimp associates were most often found distributed throughout the experimental sea tables, and were intermittently found next to an anemone. Small post-settlement *O. pictus* showed a distinct preference for *U. lofotensis*, but during some trials they did not associate with anemones (Table 14). Two fish were captured and ingested by *U. piscivora* during host preference experiments.

Field preference experiments resulted in both juvenile and adult *O. pictus* showing a preference for *U. lofotensis* ($P<0.025$, $n=6$, Chi-square test). Of two plots containing three species of anemones, all but one fish was observed with *U. lofotensis*. One adult male was observed on two occasions with the same individual of *U. piscivora*, and no fish were found with individuals of *Anthopleura xanthogrammica*.

Both field and laboratory preference experiments using model anemones resulted in no fish being observed with either the rubber models or concrete base and rubber tubing models. Laboratory preference experiments between rubber models and single individuals of *U. lofotensis* showed that fish associated with either the anemones (3 out of 6 trials), or did not associate with either the anemones or the models (3 out of 6 trials). The fish were observed near the models during the day, which suggested that

Table 14. Laboratory preference experiments with 32 small post-settlement *Oxylebius pictus* (<6 cm total length) and seven species of sea anemones. One trial for each fish. Observed values are significantly different from expected, chi-square=110.5, $P<0.001$.

Anemone species	Number of times chosen
Urticina lofotensis	23
Urticina crassicornis	2
Urticina piscivora	1
Urticina columbiana	0
Urticina coriacea	0
Anthopleura xanthogrammica	0
Metridium senile	0
no choice	6

they did not have any aversion to the models. Four nightly examinations of 10 concrete and rubber tubing models placed out in the subtidal at Helby Island did not reveal any fish associates. Field experiments involving the removal of host anemones and subsequent replacement with model anemones also resulted in no fish associating with the models. Trials were done with 4 rubber models and 5 concrete and rubber tubing models. Of the 9 *O. pictus* which were observed to associate with the host anemones, only 1 was found in the same general area when the models were examined for associaties the night of the removal. The other fish were either not found (5 individuals) or were observed with anemones located nearby. All *O. pictus* were present at control anemones which were not removed (6 individuals). These experiments suggested that individuals of *U. lofotensis* possessed other qualities besides their 3-dimensional structure which caused the fish to associate with them.

The presence of copepods on *U. lofotensis* was important in the host preference behavior of small post-settlement *O. pictus*. Fish given a choice between anemones with and without copepods spent more of their time on the anemone with copepods. The fish fed on the copepods during the day, and most fish settled next to the column of these anemones at night. Seven fish settled next to the anemones with copepods, and 1 fish chose the anemone without copepods ($P<0.01$, $n=8$, Chi-square).

Tentacle adhesion experiments

Laboratory experiments confirmed that among the fishes tested, only *O. pictus* was able to contact the tentacles of host anemones without eliciting nematocyst discharge. The tentacles of all five species of *Urticina* adhered to the other species of associated fishes during adhesion experiments. The relative adhesive forces of the tentacles of each anemone species on the fishes was significantly different (Table 15). *Urticina piscivora* and *U. columbiana* had the strongest adhesive forces of the

Table 15. Adhesion of *Urticina* anemones to different fish species. Force=Newton X 10^{-3}. (Mean ± s.d.). Number of trials in parentheses. Kruskal-Wallis tests for all comparisons. *NC*=not calculated.

	Oxylebius pictus (mucus intact)	*Oxylebius pictus* (no mucus)	*Artedius harringtoni*	*Jordania zonope*	*Coryphopterus nicholsii*
Urticina piscivora	16.7 ± 21.6 (10)	383.2 ± 223.4 (22)	167.58 ± 148.0 (11)	164.6 ± 56.8 (6)	180.3 ± 45.1 (5)
Urticina columbiana	0 (10)	234.2 ± 109.7 (7)	207.8 ± 102.0 (8)	198.0 ± 89.2 (6)	171.5 ± 84.3 (6)
Urticina crassicornis	0 (10)	156.8 ± 100.0 (18)	54.9 ± 52.9 (13)	102.0 ± 60.8 (5)	98.0 ± 22.5 (5)
Urticina coriacea	0 (10)	130.3 ± 68.6 (15)	34.3 ± 40.2 (8)	25.5 ± 24.5 (5)	70.6 ± 47.0 (5)
Urticina lofotensis	0 (10)	103.9 ± 82.3 (20)	63.7 ± 29.4 (11)	51.9 ± 15.7 (6)	102.0 ± 41.1 (5)
P	*NC*	<0.001	<0.001	<0.0.001	<0.05

anemones, while *U. lofotensis* had a relatively weaker adhesive force than either of these species.

The epidermal mucous coating of *O. pictus* appeared to be involved in the ability of the fish to acclimate to anemones. When the mucous coating of the fish was removed, the tentacles of the anemones adhered strongly to the fish (Table 15). Fish which had their mucous coating intact did not elicit nematocyst discharge by the anemones, except for small post-settlement fish which were occasionally stung by *U. piscivora*. Only four out of the ten *O. pictus* used in these trials elicited nematocyst discharge and subsequent tentacle adhesion by *U. piscivora*. The other specimens of *O. pictus* only caused contractions of the tentacles or no reaction at all on the part of the anemones.

The eggs and larvae of *O. pictus* elicited nematocyst discharge upon contact with the tentacles of anemones. When larvae were introduced into aquaria containing *U. lofotensis* and *U. piscivora*, the fish were stung and killed when they came into contact with the tentacles of the anemones. The larvae did not show signs of acclimation behavior.

Only one of five small post-settlement *O. pictus* which were separated from their hosts for at least 3 days appeared to go through a period similar to that of acclimation of tropical anemone fishes (Mariscal, 1971). The fish was stung upon initial contact with the tentacles of *U. lofotensis*, but within a few hours it was observed in the tentacles without being stung. The 4 other fish were not stung upon initial contact with anemones, and directly entered the tentacles. Fish which had their mucous coating removed appeared to approach anemones more cautiously than normal, and were apprehensive about touching the tentacles of the anemones. Fish which came into initial contact with *U. lofotensis* were able to swim away and free themselves from the anemone's tentacles. The fish then contacted the tentacles of the anemones repeatedly, and were often stung. After approximately one day they were able to enter the tentacles without eliciting nematocyst discharge or any other reaction by the anemones. It is suspected that the *O. pictus* were able to reacclimate to anemones once the fish secreted more epidermal mucus, but measurements of mucus secretion were not conducted. Small post-settlement *O. pictus* (with mucus removed) which contacted the tentacles of *U. piscivora* were stung, and sometimes captured and ingested (2 fish out of 5 trials).

Predator populations

Many different species of large fishes, which were potential predators on the associates of sea anemones, were present at Blackfish and Ohiat Islets (Table 16). The abundances of some fish species differed significantly between sites, and the overall densities of predatory fishes at the two sites were also different. The most common fishes at both sites were *Hexagrammos decagrammus* and other rockfish species. The other fishes were only present in small numbers and were counted in a small proportion of the surveys. There was a seasonal trend in the overall abundances of the fishes, with highest densities being observed in the fall, during October and November (Fig. 24).

The distributions, abundances, and activity patterns of the fishes were different between day and night. Most fishes were more abundant in transects at night than during the day (Table 17). These differences in abundance were related to the sheltering behavior of some fishes which were not detected in crevices. Also, shifts in the vertical distributions of the fishes between day and night (Table 18) resulted in some pelagic species being outside of the transect areas during the day. Their numbers would then increase at night when they returned to the reef. Most fish species were diurnally active; in the water column or on the surface of the substratum during the day, and in crevices or inactive on the surface of the substratum at night. These fishes had positive values of Δ h, which is a measure of the magnitude of shifts

Table 16. Abundances of large fishes at Blackfish and Ohiat Islets. Wilcoxon sign-rank tests for paired observations by month.

	Number of fish / 100 m^2		
	Blackfish	Ohiat	*P*
Hexagrammos decagrammus	4.6 ± 2.1	8.7 ± 4.4	<0.01
Ophiodon elongatus	1.0 ± 0.8	0.3 ± 0.6	<0.05
Sebastes melanops	3.8 ± 2.4	10.6 ± 3.7	<0.01
Sebastes nebulosus	0.7 ± 0.4	4.4 ± 1.6	<0.01
Sebastes maliger	5.9 ± 5.5	2.9 ± 2.7	<0.05
Sebastes flavidus	8.8 ± 9.0	5.3 ± 4.5	>0.10
Sebastes caurinus	2.4 ± 2.7	1.2 ± 1.2	>0.05
Sebastes pinniger	0.2 ± 0.5	0.1 ± 0.2	>0.10
Hemilepidotus hemilepidotus	0.7 ± 0.7	1.0 ± 0.9	<0.10
Total	27.8 ± 14.2	34.4 ± 15.9	<0.01

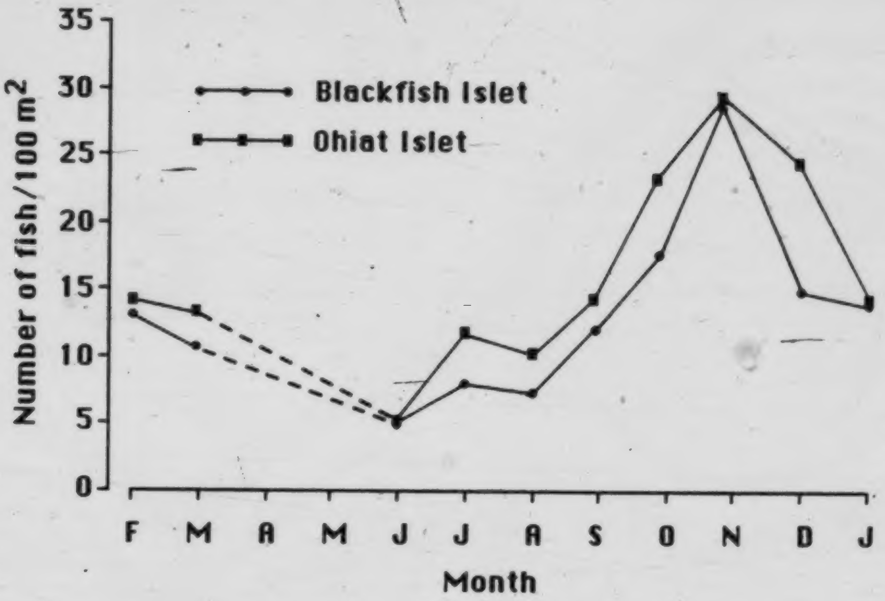

Figure 24. Seasonal abundances of large fishes at Blackfish and Ohiat Islets.
- - - - - - refers to months when surveys were not conducted.

Table 17. Day-night differences in the abundance of large fishes. Samples from Blackfish and Ohiat Islets combined. Wilcoxon sign-rank tests for paired monthly comparisons on totals for each month. *NC*=not calculated because of insufficient sample size.

	Total number of individuals		Percent of total no. of individuals		
	Day	Night	Day	Night	*P*
Hexagrammos decagrammus	141	97	35	13	>0.05
Ophiodon elongatus	18	7	4	1	<0.05
Sebastes melanops	70	188	18	26	<0.05
Sebastes nebulosus	24	67	6	9	<0.01
Sebastes maliger	27	133	7	18	<0.05
Sebastes flavidus	97	156	24	22	>0.10
Sebastes caurinus	17	47	4	6	>0.10
Sebastes pinniger	2	3	<1	<1	*NC*
Hemilepidotus hemilepidotus	4	26	1	4	<0.05
	—	—	—	—	
Total no. of individuals	400	724	100	100	

Table 18. Vertical distribution of large fishes during the day and night. Vertical zones defined in Table 1. The Δ h measure of a species change in vertical position is defined in the text.

	Day				Night				
	Mid-water	Supra-benthic	Bottom	Shelter	Mid-water	Supra-benthic	Bottom	Shelter	Δ h
Hexagrammos decagrammus	3	86	47	5	0	9	53	35	0.89
Ophiodon elongatus	0	6	10	1	0	1	4	2	0.44
Sebastes melanops	4	46	10	11	1	31	40	116	1.05
Sebastes nebulosus	0	4	3	17	0	0	23	44	0.12
Sebastes maliger	1	11	5	10	0	33	64	36	0.13
Sebastes flavidus	7	73	1	16	42	59	32	23	-0.04
Sebastes caurinus	0	4	4	9	0	22	14	11	-0.53
Sebastes pinniger	0	2	0	0	0	2	0	1	0.67
Hemilepidotus hemilepidotus	0	0	2	2	0	1	17	8	-0.23
Total	15	232	82	71	43	158	247	276	
Percent of total	4	58	20	18	6	22	34	38	
Number of transects	40	40	40	40	40	40	40	40	

in vertical distribution (Ebling and Bray, 1976). The statistic ranges from a maximum shift downward from the mid-water zone during the day to crevices at night (+3.0), to a maximum shift up from shelter during the day to mid-water at night (-3.0). The fish with the most pronounced nocturnal pattern of activity was *Hemilepidotus hemilepidotus*. This species was only rarely observed during the day, but individuals emerged from shelter during twilight and were conspicuous members of the reef at night. *Sebastes caurinus* and *S. flavidus* were also observed to be active at night. Juveniles of *S. flavidus* were usually inactive during the day, but became more active at night. *Sebastes maliger* and *S. nebulosus* had relatively low positive Δ h values, and were often observed to be active during night surveys. All of the fishes except *H. decagrammus* foraged most intensely during twilight.

Other potential predators observed at the study sites were *Octopus rubescens*, *O. dofleini*, and juvenile *Anarrhichthys ocellatus*. These 3 species were often observed during night dives at both Blackfish Rock and Ohiat Islet, but were most abundant at the Harbor Limit. The octopuses and wolf eels were usually observed foraging or sheltering in holes or rock crevices.

Predation Experiments

Predation experiments with both piscivorous fish species and *Octopus rubescens* showed that: 1) small *O. pictus* were more vulnerable to predators than large fish, 2) *U. lofotensis* provided effective shelter space for the fish, and 3) anemones may provide more effective shelter than rock holes or crevices from some species of predators. Most small *O. pictus* (3-5 cm total length) were eaten by predators in the absence of host anemones, and those fish associated with anemones were usually not preyed upon (Tables 19, 20). Large *O. pictus* were not preyed upon by *O. rubescens*, but one large fish (11 cm total length) was eaten by a large *S. caurinus* (30 cm total length). One small *O. pictus* was eaten by *S. maliger* in the presence of a

Table 19. Predation experiments with *Octopus rubescens* (4-7 cm mantle length) and small and large *Oxylebius pictus* in the presence and absence of *Urticina lofotensis.*

	no. of fish eaten (no. of trials)	
Fish	Without anemone	With anemone
Small *Oxylebius pictus* (3-6 cm total length)	14 (16)	2 (14)
Large *Oxylebius pictus* (> 10 cm total length)	0 (10)	0 (0)

Table 20. Laboratory predation experiments with the piscivorous fishes *Sebastes caurinus, S. maliger,* and *Hemilepidotus hemilepidotus* (15-30 cm, total length) and the prey *Oxylebius pictus* in the presence and absence of *Urticina lofotensis.*

	no. of fish eaten (no. of trials)	
Fish	Without anemone	With anemone
Small *Oxylebius pictus* (3-6 cm total length)	15 (15)	1 (15)
Large *Oxylebius pictus* (>10 cm total length)	0 (6)	1 (6)

host anemone. The rockfish was observed to approach the *O. pictus*, which responded by swimming out from under the tentacles of its anemone and eventually being chased down and eaten. The small individuals of *O. pictus* which were eaten by octopuses did not appear to associate closely with anemones. Specimens of *O. rubescens* were observed trying to capture small *O. pictus* during the day, but they were unsuccessful during the attempts seen. The octopuses were successful, however, when the fish were inactive at night and sheltered in holes between the rocks in the aquarium. The piscivorous fishes would usually prey upon the small *O. pictus* within minutes to hours after the predators were put into the tanks, but the octopuses would often take days to weeks to feed on a fish. Specimens of the crab *Scyra acutifrons* were also fed to the octopuses. The octopuses readily fed upon the crabs which did not associate with anemones.

Anemone transplant and removal experiments

The densities of *O. pictus* did not differ significantly between the control and treatment plots at the Harbor Limit study site during initial surveys in 1984 (Table 21). After these surveys, 30 *U. lofotensis* were transplanted into each of the two replicate treatment plots in late August 1984. Examinations of these anemones at night over the next six months revealed that many *O. pictus* associated with the anemones (Fig. 25). Most of the *O. pictus* were small post-settlement fish, and up to seven individuals were found with one anemone. The number of associated fish per anemone was over three times greater at the Harbor Limit transplant site than at Blackfish or Ohiat Islets. The population densities of *O. pictus* were also much higher at the Harbor Limit (Table 2). Many of the anemones were not found in the transplant areas after six months. Only 10 anemones were located in one treatment site after six months, and 15 anemones were found in the other. Some of the losses were probably from difficulty in locating the anemones amongst the rock boulders,

Table 21. Mean population densities of *Oxylebius pictus* observed in control and treatment plots at the Harbor Limit study site during surveys conducted in late August, 1984, and September 1985. Treatments were 2 replicate plots each containing 30 transplanted *Urticina lofotensis* . Controls were 2 replicate plots without anemones. Population densities were determined from 2 separate transects in each treatment and control plot. Each transect was sampled 2 times on separate days in 1984, and three times in 1985. Totals of the samples for each transect were used in statistical comparisons. (*n*=4 for treatments and control). Mann-Whitney U-tests for comparisons between controls and treatments.

	(Mean no. of fish / 100 m^2 ± s.d.)		
	Control	Treatment	*P*
1984			
totals	4.1 ± 1.2	4.4 ± 1.6	> 0.1
adults	2.8 ± 0.8	3.1 ± 0.9	> 0.1
juveniles	2.1 ± 1.4	1.4 ± 1.1	> 0.1
1985			
totals	4.3 ± 1.1	7.2 ± 2.1	$0.05<P<0.1$
adults	2.9 ± 0.5	2.9 ± 1.2	> 0.1
juveniles	1.1 ± 0.5	3.9 ± 1.1	$0.01<P<0.05$

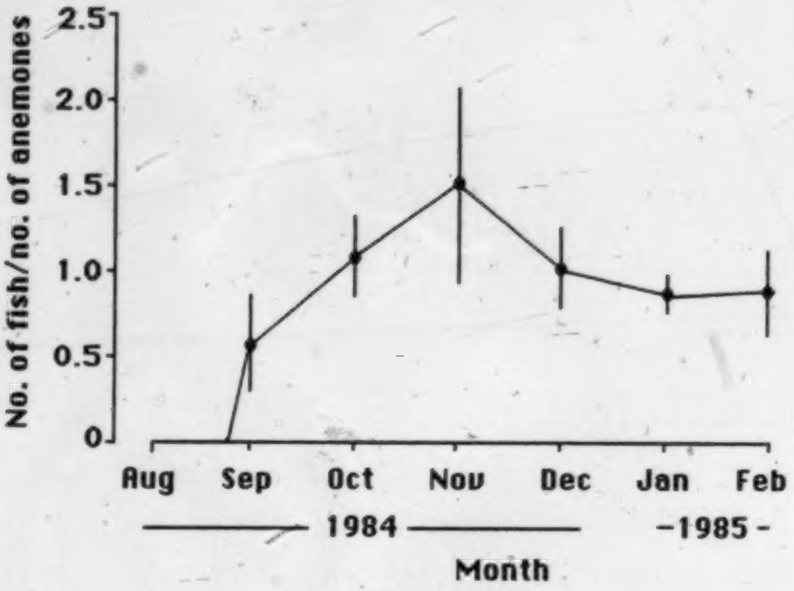

Figure 25. The total number of *Oxylebius pictus* associated with *Urticina lofotensis* / total number of *Urticina lofotensis* transplanted in two treatment plots at the Harbor Limit. Each treatment plots contained 30 anemones which were transplanted in August of 1984.

but many individuals probably died from tissue damage which occurred while they were being transplanted.

Fish population surveys were made of both the control and treatment plots in September of 1985. There was not a significant difference in the overall density of *O. pictus* between the the treatment and control sites, but there was a difference in the density of juvenile fish (Table 21). The juvenile fish were all members of the size class which had recruited the previous fall. The number of adult fish in the treatment plot was not significantly different from the control plot.

Daytime removal of 32 *U. lofotensis* (which had associated *O. pictus* the previous night) in the fall of 1985 resulted in only 16 percent of the *O. pictus* returning to the site where their host anemone was removed. The rest of the fish were either found at anemones nearby (34%), or were not found within 2 m of the removal sites (50%). All fishes were present at the 8 control anemones which were not removed. Surveys done one month later during the day and night resulted in no fish being found at the removal sites.

DISCUSSION

Many physical and biological factors influenced the distributions and abundances of the anemones and their associates. The following discussion will identify these factors, and illustrate the various relationships between the associates and their host anemones. Predation appeared to be very important in determining the association patterns between the organisms, and the discussion will begin with a description of the predators in the system. The ecology of the host anemones will then be described, followed by an autecological analysis of each associated species. The majority of the discussion will center on the association between *O. pictus* and *U. lofotensis* since this relationship was studied most intensely. The other associations will be discussed in less detail. These autecological analyses will put the results of the study in perspective and provide the basis for a general discussion of the relevance of anemone associations to the study of symbioses.

Predators of anemone associates

Many species of organisms which are predators of anemone associates were present at all of the study sites. The most important predators were large fishes. *Hexagrammos decagrammus* was abundant at both study sites, and large numbers were present all year around. It is a generalist feeder which preys on whatever is available, mostly benthic crustaceans, and holothuroids (Moulton, 1977), but it also feeds on small benthic fishes. This predator feeds during the day and during twilight but is inactive at night (Moulton, 1977). Another hexagrammid fish present at the sites, *Ophiodon elongatus*, is also diurnally active. It feeds almost exclusively on other fishes (Hart, 1973; Moulton, 1977; Eschmeyer et al., 1983).

The rockfishes *Sebastes melanops* and *S. flavidus* feed mainly on pelagic fish and crustaceans (Leaman, 1976; Moulton, 1977), but *S. melanops* also preys heavily on benthic species of shrimp (Moulton, 1977). These fish are crepuscular predators, feeding most actively during dawn and dusk (Moulton, 1977). *Sebastes melanops* was most abundant during night surveys. This is the result of fishes being active in open water during the day and returning to reef areas at night where they rested on the surface of the substratum or in crevices. *Sebastes pinniger* is also a pelagic feeder (Moulton, 1977), but it was rarely observed at the study sites.

The three other species of rockfishes, *S. maliger*, *S. caurinus*, and *S. nebulosus*, are all benthic species which are mainly crepuscular predators, but are also active during the day and night (Moulton, 1977; McElderry, 1979). They all feed on benthic crustaceans and fishes. Details of their feeding habits will be described in later sections on their particular prey species.

Hemilepidotus hemilepidotus was the only fish species which had a distinct nocturnal pattern of activity. During the day individuals hid in crevices, and emerged to forage over the reef at night. This behavior has also been documented by DeMartini and Patten (1979). Feeding habits are described in DeMartini and Patten (1979), and major prey items are crabs (including *S. acutifrons*), shrimps, and small cottids (*Artedius* spp.).

It is clear that the fishes which are present at the study sites feed heavily on the associates of the anemones. The predation pressure exerted by these fishes is likely a strong selective force molding not only the diel behavior patterns of the associates, but also their choice of refuge sites. The effects of other predators which were relatively less abundant at the study sites, such as octopuses, are likely not as large as those of the fishes. However, the predatory effects of octopuses are probably much different from those of most fish species because of the octopuses' different feeding habits, and their ability to enter all types of holes and crevices to capture their prey. Juvenile *Anarrhichthys ocellatus* are also well adapted to entering holes and crevices to pursue their prey (Eschmeyer et al., 1983).

Anemones

Urticina lofotensis was most abundant in exposed habitats, and was rare to absent in protected areas with little wave action. *Urticina piscivora* was present at all study sites. These distribution patterns may be due to the effects of exposure on the feeding success of the anemones. Anemones are opportunistic feeders, and they can only prey on whatever organisms come in contact with their tentacles. Stomach content analysis of *U. lofotensis* indicates that it feeds on mostly small benthic crustaceans and sessile invertebrates which have been detached from the substratum (Sebens and Laakso, 1978; Elliott and Warren, in prep.). *Urticina piscivora* preys on the same types of organisms except that it also has the ability to catch small fishes and swimming scallops with its strongly adhesive tentacles. The feeding posture and habitat selection of the anemones reflected their different feeding habits. The tentacles of most *Urticina lofotensis* extended down close to the substratum, and individuals were distributed evenly between open rock areas and crevices. In contrast, most *U. piscivora* were in open rock areas on the tops of boulders or rock prominences with their tentacles extended up into the water column. Both species of anemones were usually oriented with their oral disks facing in an upward direction, facilitating the capture of prey coming down from above them. The greater abundance and availability of prey in exposed habitats may explain why *U. lofotensis* was found more commonly in these areas. Heavy wave action dislodges animals from the substratum, and increases their chance of contacting the tentacles of an anemone. The feeding habits of *Urticina piscivora*, however, allowed it to utilize planktonic prey items which were available in all study habitats.

At Blackfish Islet, the anemones were most abundant in shallow water (0-3 m), but at Ohiat Islet there were few *U. lofotensis* and no *U. piscivora* at those depths. Both species were abundant from depths of 3-18 meters at Ohiat Islet. This likely reflects the food availability at different depths in relation to the amount of food transported to deeper water by wave action. Wave exposure may also physically damage anemones which are in shallow water at Ohiat Islet. These anemones are not adapted for survival in high wave stress areas as is *Anthopleura xanthogrammica* (Koehl, 1976) which was abundant in shallow water at this site. By living in deeper water species of *Urticina* avoid the full impact of waves.

Predation by starfish is important in determining the distribution and abundance of anemones (Sebens, 1977; Elliott et al., 1985). Few small individuals were found in the populations of either *U. lofotensis* or *U. piscivora*. These were the only anemones which disappeared from the study sites, which was probably due to the high predation pressure on small anemones by either *Dermasterias imbricata* or substratum grazers, such as the sea urchin *Strongylocentrotus franciscanus*. Large *U. lofotensis* and *U. piscivora* have a refuge in size from *Dermasterias imbricata* (Elliott et al., 1985). Small *U. piscivora* have an escape response to the starfish, but individuals of *U. lofotensis* do not. Small anemones may also have a refuge from *D. imbricata* by settling next to large individuals, as do small sea urchins (Duggins, 1981). Many sessile organisms in the rocky intertidal only persist in crevices, where they have a refuge from predators (Menge and Lubchenco, 1981). Eighty percent of *U. lofotensis* smaller than 4 cm oral disk diameter were attached in rock crevices, and the other 20 percent were found next to large anemones.

All large individuals in the populations were present in the same locations after 18 months. Large individuals of *Anthopleura xanthogrammica* are also known to persist in the same locations for long periods (Sebens, 1977). This suggests that these species are very long-lived, as is the case for most species of anemones (Allen, 1975; Sebens, 1977). *Urticina lofotensis* and *U. piscivora* therefore provide an abundant, stable, and virtually permanent source of shelter area for organisms which have the behavioral or physiological capabilities to associate with anemones.

Oxylebius pictus

Herald (1972) was the first to report that *Oxylebius pictus* had the ability to contact the tentacles of *Urticina* anemones without being stung, but no field studies were carried out to determine if the fish associated closely with anemones in the natural environment. Results from this study show that the association does occur in areas of Barkley Sound where the fish and sea anemones distributions overlap. The association is facultative since both the fish and the anemones are able to survive in the absence of the other.

The anemones benefit *O. pictus* by modifying existing interactions between the fish and its food resources and predators. Food is not considered to be a limiting resource for most populations of *O. pictus* (DeMartini, 1976). All of the fish collected for stomach content analysis had something in their guts, which suggests that there were adequate food resources in the habitats. Large *O. pictus* fed on amphipods, crabs, copepods, and other small benthic crustaceans, as has been reported in previous studies (DeMartini, 1976). Small *O. pictus* fed almost exclusively on copepods and amphipods. The crustacean associates of the anemones contributed to only a small proportion of the diets of large fish, but the copepod *D. sunnivae* made up one fourth of the diets of small fish. This is the first documented evidence of fish utilizing other associates of a host sea anemone as a regular food resource. Mariscal (1970) suggested that copepod associates of tropical anemones may serve as a food source for juvenile *Amphiprion*, but are probably not important in the diet of large adults. He described the nibbling behavior of *Amphiprion* species on the tentacles of the anemones, and speculated that the fishes may actually be feeding on associated copepods. Cyclopoid copepods are probably the most common crustacean associates of anemones (Briggs, 1976; Gotto, 1979; Humes, 1982; Lønning and Vader, 1984), and their small size and often cryptic color patterns make them hard to distinguish on their hosts. Some of the observations of tropical anemone fishes feeding on the mucus and tissues of host anemones may have been misinterpreted, and the fishes may have actually been preying on associated copepods.

Laboratory experiments showed that a fish could remove most of the copepods from an individual *U. lofotensis* within a few days. To maintain a constant source of these copepods in the field, fish must either feed intermittently on the copepods from one anemone, or feed from several anemones. Recruitment of copepods during the late summer may be high enough to maintain populations despite the foraging of fish, but in the fall *O. pictus* reduced the copepod populations on host anemones, causing an intrinsic shortage of this food resource for small post-settlement fish. The fish then had to seek food sources away from the protective shelter of their host anemones.

Protection from predators is considered to be the major benefit that fishes gain by associating with anemones (Allen, 1975; Mariscal, 1970, 1972; Fautin Dunn, 1981). Obligate anemone fishes which are caught and released away from their host anemone are readily preyed upon by other piscivorous fishes (Mariscal, 1970). Also, when host anemones are removed, the anemone fishes are pursued and eaten by predatory reef fishes (Mariscal, 1966). In areas where predators are not abundant, anemone fishes venture long distances away from their host anemones without a high risk of being preyed upon (Moyer, 1980). Facultative fish associates are also assumed to benefit from reduced predation pressure by sheltering in the tentacular sphere of anemones (Colin and Heiser, 1973; Smith, 1973; Hanlon and Kaufman, 1976; Hanlon et al., 1983). Only fishes most vulnerable to predation, such as juveniles or individuals of small species, are facultative associates. As the fishes grow larger they do not associate closely with anemones, but use other structural reef components for shelter.

As in other facultative associations, small *O. pictus* were observed to associate more closely with anemones than large fish. Juvenile *O. pictus* have also been observed associating with gorgonians in California (Feder et al., 1974). Predation by relatively larger piscivorous fishes has been shown to cause small fish to remain in sheltered areas, whereas large fish forage out in the open (Werner et al., 1983). Small post-settlement *O. pictus* spent much of their time with host anemones during the day. Larger juvenile and adult *O. pictus* only associated with anemones at night when the fish became inactive. Some adults did not associate with anemones, but sheltered in crevices at night. These observations suggest that small inactive fish were most vulnerable to predation. Experiments with different sized individuals of *O. pictus* showed that small fish were preyed upon more readily than large fish when not associated with a host anemone. Piscivorous fish predators captured small individuals of *O. pictus* during the day, but specimens of *Octopus rubescens* appeared to be most successful at capturing small fish at night. In the field, juveniles were less attentive than adults at night and were more easily collected by a diver. Perhaps small fish are also captured more easily by nocturnal predators.

Small fish returned to their host anemones either before or during early evening twilight, and left the anemones after sunrise. Large fish usually returned to anemones during late evening twilight, and left during early morning twilight. This size related activity pattern is also seen in other fishes, where large individuals take shelter later in the evening and leave shelter earlier in the morning than small individuals (Hobson, 1972; Helfman, 1978; Hobson et al., 1981). This pattern is considered to be the result of increased predation during crepuscular periods, and the higher vulnerability of small fishes to predators (Hobson et al., 1981). Behavioral observations of the large piscivorous fish species at the survey sites indicated that they were most active during twilight. Studies of these species in other areas and at Ohiat Islet support these observations (Leaman, 1976; Moulton, 1977; McElderry, 1979).

Even though few adult fish were observed with anemones, some males associated with anemones while guarding egg masses during the spring and summer spawning period. Adult males defend spawning sites in high relief rocky areas exposed to strong water movement (DeMartini, 1986). Areas of stronger water movement provide increased aeration for eggs, which leads to faster development times (DeMartini, 1976). Adult males are probably more vulnerable to predators when they are actively guarding egg masses (DeMartini, 1986). The sites where males were associated with anemones in this study were solid rock areas without cracks or crevices in which they could shelter in, whereas most of the other males defended spawns in rock boulder areas with crevices for shelter holes. The presence of anemones in solid rock areas may provide needed shelter space for adult male fish if shelter holes are absent. However, monitoring of all males which were guarding egg masses did not indicate any distinct difference in the survival of associated and non-associated fish.

Oxylebius pictus eggs are preyed upon by many fishes (DeMartini, 1986), and the presence of an anemone may deter these predators from feeding on egg masses spawned near by. The survival of egg masses guarded by either associated or non-associated males was not closely monitored, but cursory observations suggest that there was not any distinct difference between groups. If males which associate with anemones do have "better" spawning sites, more females would be expected to spawn with these males in comparison to males with spawning sites near shelter holes. However, males associated with anemones did not have significantly larger mean number or size of spawns than non-associated males, but the maximum number of spawns was far greater for associated males (6 compared to 2). A larger sample size and measurements of hatching success are needed to substantiate these results.

Oxylebius pictus readily associated with the transplanted anemones at the Harbor Limit site where there was already abundant shelter in the rock boulder substratum. This suggests that small fish prefer to shelter with anemones rather than sheltering in rock holes and crevices. Small *O. pictus* were only immune from predation by *O.*

rubescens when the fish were associated with *U. lofotensis*. The stinging tentacles of the anemones were a strong deterent to the octopuses. Ross (1971) has also shown that symbiotic anemones protect their hermit crab hosts from octopuses. The anemones probably provided *O. pictus* with effective protection from predators which could enter holes and crevices, such as octopuses and individuals of *Anarrhichthys ocellatus*.

The quality of shelter provided by the anemones varied between individuals and different species of hosts. *Oxylebius pictus* was only found in association with two species of *Urticina*, and host preference experiments showed that *O. pictus* preferred *U. lofotensis* to other species of anemones. The tentacles of *U. lofotensis* often extended down to the substratum forming an enclosed space next to the column of the anemone. This morphological characteristic allowed *U. lofotensis* to provide more shelter space than other species of anemones which had their tentacular crowns either high above, or right on the surface of the substratum. It was difficult to observe fish which were next to the column of *U. lofotensis*, and the shelter space may have concealled the fish from predators.

Oxylebius pictus only associated with *U. lofotensis* which were larger than 6 cm, and *U. piscivora* larger than 11 cm. This selection of host anemones was probably related to the amount of enclosed subtentacular space of different sized individuals of each species, and the size of the associated fish. Since *U. piscivora* had its tentacular crown high off the substratum, only large individuals had long enough tentacles to extend down the height of the column to form an effective shelter space.

The orientation of the substratum and host anemone also influenced the shelter space provided by anemones. Individuals which were oriented with their oral disks facing downward or horizontally had less subtentacular shelter space since their tentacles did not extend down toward the substratum forming a space next to the column. More *O. pictus* associated with anemones which were on relatively horizontal substrata and had their oral disks facing upward than anemones which were on substrata of other orientations. Fish appeared to be more stable when they rested on the substratum under the tentacles, compared to when they rested on the columns or oral disks of anemones on vertical substrata.

The barrier of tentacles which formed the shelter space were a strong deterrent to potential predators. All fishes, except *O. pictus*, appeared to avoid the tentacles of *U. lofotensis* and *U. piscivora*. The strong tentacular adhesive force of *U. piscivora*, which allows it to capture and feed on fishes (Sebens and Laakso, 1978; Elliott and Warren, in prep.) may also provide better protection from predators than other anemones with weaker adhesive forces. However, small *O. pictus* were prevented from associating with this anemone since they may be caught and eaten during initial acclimation. These fish were able to acclimate to *U. lofotensis*, whose tentacles appeared to be an adequate deterrent to predators. Predators which pursue fishes into the tentacles of anemones not only risk being captured, they also risk being stung and having their epidermis damaged by the anemone's nematocysts and spirocysts.

Small post-settlement fish are probably most vulnerable to predation when foraging in areas away from shelter, whether it be a crevice or their host anemone. Since the copepods on the anemones are a source of food, small fishes can feed on these copepods and be protected from predators at the same time, reducing the amount of time spent away from shelter. During periods of high copepod densities the fish may never have to leave their host anemones for food, but during the fall when copepod densities decrease, fish must venture away from their anemones for food. The observations in this study suggest that the fish do spend less time with their anemones in the fall once copepods numbers are reduced.

The presence of cohabiting individuals can also affect the amount of time a fish must spend away from shelter. When more than one fish associated with the same host anemone, larger fish chased smaller individuals away during daytime encounters. Small *O. pictus* were able to cohabit anemones with larger fish either by returning during twilight, or by staying on a separate part of the anemone away from the larger fish. The behavior of small fish to remain on the oral disk of an anemone at night may be partially due to intraspecific aggression since 75 percent of all *O. pictus* observed on the oral disk at night were on host anemones with another fish beneath the tentacles. One pair of fish which remained together on a host anemone for over four months were always found with the larger fish next to the column of the anemone, and the smaller fish on the oral disk. This partitioning of space on the anemone may have reduced the number of aggressive encounters, and allowed the two fish to share the same host. Once fish attained larger sizes during the winter, they became more territorial. This resulted in usually one fish being found on the same host from March to June.

It has been shown that the anemones benefit the fish by deterring predators and increasing prey availability, thereby modifying existing predator-prey interactions. These benefits are at the individual level, but they do not necessarily lead to beneficial effects at the population level in mutualistic associations (Addicott, 1985). Benefits may arise at the population level in either faster growth rates or increased population density. The effect of individual level benefits on population density are dependent on the "complexity of the mutualism, whether an organism associates with its mutualist for a small or large part of its life history, and whether the mutualist is able to increase the availability of a limiting resource" (Addicott, 1985). Food resources do not appear to be limiting to *O. pictus* populations (DeMartini and Anderson, 1980), but the presence of a food source on host anemones allows small post-settlement fish to remain on or near their anemone without having to venture farther away for food where they are more open to predators. Predation on small post-settlement fish is assumed to be the major factor limiting *O. pictus* population density

(DeMartini, 1976). Since the fish associate closely with anemones at this critical life history stage, there may also be beneficial effects at the population level.

Predation has been shown to be important in regulating population densities of prey species in aquatic habitats (Sih et al., 1985), especially in fish communities (Werner et al., 1983). Studies by DeMartini (1976) and DeMartini and Anderson (1980) presented indirect evidence for predator limitation of *O. pictus* population densities in Puget Sound, Washington, and Monterey Bay, California. The higher diversity and abundance of predators in the Monterey Bay area was assumed to be the main determinant of the populations' skewed size distribution towards more juveniles, and smaller maximum size and shorter life span of adult fish. The size and estimated age distributions of *O. pictus* populations in Barkley Sound were most similar to the Monterey populations. A comparison of *O. pictus* population densities at different sites in the north Pacific indicate that there are fewer fish and a higher proportion of juveniles in areas where predators are most abundant. DeMartini and Anderson (1980) reported *O. pictus* density for the Shilshole Breakwater, Washington (36.0 ± 2.0, mean number of fish per 100 m^2 ± S. E., n=27 transects), where predators were rare, and densities at two other sites where predators were abundant; Keystone Jetty, Washington, (4.0 ± 0.04, n=9) and Powell River, British Columbia (2.0, n=1). DeMartini (1976) suggests these population density patterns are a result of the differential predation rates in the areas. A comparison of these *O. pictus* densities with those for populations in Barkley Sound (Table 2) indicates that the Harbor Limit population density was similar to the one at Keystone Jetty. The population densities at Blackfish and Ohiat Islets were similar to the Powell River site.

The relatively low population densities of *O. pictus* in Barkley Sound may be due to the high diversity and abundance of predators in this region (refer to discussion of predators). Predation on small post-settlement *O. pictus* has been reported for piscivorous fishes (Burge and Schultz, 1973; Larson, 1972), and for one bird species, Brandt's cormorant, *Phalacrocorax penicillatus* (DeMartini and Anderson, 1980).

The differences in population densities between sites in Barkley Sound may also be related to the diversity and abundance of predators. The Ohiat Islet site had a greater abundance of piscivorous fishes than Blackfish Islet (Table 2). This may explain the lower survival rates of first year *O. pictus* at Ohiat Islet (7 % over 1 year) compared to Blackfish Islet (30 % over 1 year). Survival rates of other age classes were not accurately measured, but they were assumed to be higher for larger fish. Many of the adult males remained in the same areas for the duration of the study. The population density of *O. pictus* was highest at the Harbor Limit, and the density of piscivorous fishes was lowest at this site. There was a higher density of octopuses at this site compared to both Blackfish and Ohiat Islets, but laboratory predation experiments in this study and reports of their feeding habits suggest that they do not prey heavily on fishes (Hartwick et al., 1980).

The amount of wave exposure and shelter space at the different study sites in Barkley Sound may also affect *O. pictus* population densities. *Oxylebius pictus* is known to be more abundant in habitats protected from open oceanic swell (DeMartini, 1976; Eschmeyer et al., 1983), and this was supported by density surveys at different sites (Table 2). Fish densities were highest at the Harbor Limit, which is a protected site, and densities were lower at Blackfish and Ohiat Islets which were exposed to higher wave action, respectively. More fishes associated with anemones in deeper water at Ohiat Islet (Table 4), where the effects of wave surge were not as great compared to shallow water.

Experiments in aquatic communities have shown that habitat structural complexity is important in regulating prey densities (Sih et al., 1985). The differences in structural complexity between habitats in Barkley Sound may also explain the different population densities of *O. pictus* in these areas. At the Harbor Limit, where *O. pictus* densities were highest, the substratum was composed of rock boulders which had many holes for the fish to shelter in. The Blackfish Islet site had a similar rock boulder bottom in shallow water nearest Helby Island, but towards the Trevor channel side of the islet the substratum was composed of mostly solid rock (Fig. 3). The solid rock areas did not have as many potential shelter holes for the fish, and many of the crevices were frequented by large piscivorous fish species. At the Ohiat Islet site, the substratum was mostly solid rock with a small boulder area at one end of the study site at a depth of 20 m (Fig. 2). Most of the large juveniles and adults were observed in the boulder area. The predominance of a solid rock substratum, which offered little shelter space for the fish, may be one explanation for the low densities of *O. pictus* at Blackfish and Ohiat Islets. The anemones were an important source of shelter space for the populations of *O. pictus* in these habitats. The importance of shelter is further supported by the low densities of *O. pictus* at Aguilar Point. The combination of a solid rock substratum and low densities of *U. lofotensis* in shallow water at this site suggests that the availability of effective shelter space may limit the population densities of *O. pictus*.

Manipulation experiments in other aquatic systems have shown an increase in prey density with an increase in the abundance and quality of refuges (Crowder and Cooper, 1982; Gilinsky, 1984). The transplant experiment at the Harbor Limit was conducted to test if an increase in anemone density would have an effect on the population density of fish in areas where there were previously very low densities of anemones. The experiment did not result in a significant increase in the overall population density of *O. pictus* in transplant plots compared to control plots from 1984 to 1985. However, there was a difference in the density of juvenile fish between the transplant and control plots. These fish were of the size class which recruited the previous fall and associated with anemones in the transplant plots. Since juvenile *O. pictus* benefitted most by associating with sea anemones, this density increase may reflect the increased survivorship of small post-settlement fish in transplant plots as compared to control plots. There was no significant change in the density of the adult fish, and it is not known if the increase in juvenile fish would eventually affect the density of adult fish in two or three years when the juveniles matured. But even if the short term increase in the abundance of juveniles has no effect on the future equilibrium density of the population, the increased survival of juveniles may have a significant effect on population growth rates. The association may be more important at population densities below equilibrium levels, affecting the rate at which the population could recover from a perturbation (Addicott, 1985; Wolin and Lawlor, 1985). The increased survival of small post-settlement fish in areas with anemones may allow a quicker recovery from low population densities or years of low recruitment. Recruitment of *O. pictus* was quite variable for the two years of study, and increased survival of small post-settlement fish which associate with anemones may reduce population fluctuations between years. Recruitment is also variable in other northern populations of *O. pictus* (DeMartini, 1976).

The results of the transplant experiment may also be interpreted as being caused by higher recruitment of small post-settlement fish in plots with anemones than plots without anemones. At Blackfish and Ohiat Islets, newly recruited fish were ony found with anemones. The fish appeared to preferentially settle with anemones in these habitats, and they probably searched for a host before they settled out of the plankton. At the Harbor Limit, larval fish may have also searched for hosts over the scale of the experimental area, with most individuals settling in areas with anemones. Unfortunately, population estimates of recruitment were not conducted, primarily because of the difficulty in locating small post-settlement fish in the rock boulder habitat. However, it appears evident that selective larval settlement allows *O. pictus* to locate their hosts over at least a small spatial scale, and may have profound effects on recruitment in a particular habitat.

Removal experiments demonstrated that areas which were suitable for individuals of *O. pictus* when host anemones were present were deserted when anemones were removed. Some of the fish moved to nearby anemones, but other fish were either preyed upon by predators, or moved to areas away from the removal sites. Fish which returned to the removal sites the first night of the experiment were left out in the open without shelter. These fish were likely preyed upon if they did not find shelter in other areas.

Other associated fishes

The fishes *Artedius harringtoni*, *Jordania zonope*, and *Coryphopterus nicholsii* did not associate closely with anemones. These fish species were only found intermittently with *U. lofotensis* and *U. piscivora*, while most individuals in the populations sheltered in crevices or amongst other sessile invertebrates. Although these associations are clearly facultative, the anemones benefitted the fishes by providing protection from predators (as discussed for *O. pictus*). The shelter space provided by the anemones may be a better refuge from predators than natural shelter holes, but the cost of utilizing this space is the chance of being stung, or even captured and eaten by a host anemone. The fishes may also benefit by feeding on the crustacean associates of anemones. The results of the stomach content analyses of *A. harringtoni* and *J. zonope* were similiar to those of Moulton (1977). The fish feed mainly on crustaceans; adult and larval crabs, amphipods, and shrimps. More rigorous samping of the stomach contents of these fishes may conclusively show that they do feed on the large crustacean associates of the anemones.

The overall benefits of the shelter space varies between different species, and between different individual anemones. The fishes associated almost exclusively with

U. lofotensis, except *A. harringtoni* which also was observed in aggregations of *Metridium senile*. As for *O. pictus*, *U. lofoftensis* offered the best shelter to the fish. Also, the weak tentacular adhesive force of *U. lofotensis* would make it less costly to associate with than other *Urticina* species if the fishes accidently contacted the tentacles of their host. The orientation of the anemones was only important to individuals of *C. nicholsii*. This species of fish was usually observed resting on horizontal surfaces, but *A. harringtoni* and *J. zonope* were often observed in stable resting positions on substrata of all orientations. *Jordania zonope* is usually found in wave swept areas where it is commonly observed resting on vertical rock faces (Eschmeyer et al., 1983).

The abundance of the fishes differed seasonally, with few or no individuals associating with anemones during the months of lowest sea water temperatures from December to April. Cold winter temperatures are suggetsed to affect the activity patterns of fishes, with many species being torpid during winter months (DeMartini, 1976; Gascon, 1982). The fewer numbers of associated fishes during winter may be related to their becoming less active at this time of year and sheltering in rock holes and crevices. This pattern has been observed for *C. nicholsii* in Barkley Sound (Gascon, 1982).

The density of the fishes also differed betwen the study sites. *Coryphopterus nicholsii* was much more abundant at the Harbor Limit site than at either Blackfish or Ohiat. This was probably due to the topography and the amount of wave exposure at the different sites (as discussed for *O. pictus*). *Coryphopterus nicholsii* is most common in protected areas (Hart, 1973; Cole, 1982; Eschmeyer et al., 1983), where individuals shelter under boulders on sandy substrata.

Doridicola sunnivae

Doridicola sunnivae has an obligate relationship with *U. lofotensis* (Lønning and Vader, 1984). The copepod is dependent on the anemone for both food and protection from predators. Population densities of the copepods fluctuated seasonally, with highest densities occurring in the summer and early fall when sea water temperatures were warmest. The high correlation between these two parameters (r^2_s=0.90) suggests that temperature may be a factor affecting copepod abundance, but other environmental factors which vary seasonally probably also affect the survival or reproductive rates of the copepods. Water temperature also decreases with depth, and there was a significant correlation between copepod density and depth of the host anemones. Temperature does not appear to affect the survival of adult stages of the copepod *Paranthessius anemoniae* (Briggs, 1976), but its effects on the metabolic rate of symbiotic copepods and their assimilation of food for growth and reproduction have not been investigated. *Doridicola sunnivae* has a high fecundity (Lønning and Vader, 1984), and increased sea water temperatures may cause increased fecundity and subsequent recruitment of copepodites on to the anemones. The high reproductive potential and short generation time of *D. sunnivae* may allow it to take advantage of increased water temperatures during summer, and maintain population densities throughout the early fall.

Alternatively, the survival and subsequent recruitment of planktonic stages may also be highest during times of warm water temperatures. Phytoplankton is most abundant during summer in the Barkley Sound region, and the relatively lower food resources in winter may limit the recruitment of the copepods during this time of year.

Seasonal changes in environmental conditions may also affect the production rate of anemone mucus, which *D. sunnivae* utilizes as a food resource. Copepods densities may be limited by the amount of mucus produced by anemones at certain times of the year, or by the amount of mucus produced by anemones at different depths. Mucus production by cnidarians is also known to be dependent on the presence and activity of symbionts. When the crustacean symbionts of the coral *Pocillopora* are removed, the amount of mucus produced by the coral decreases (Glynn, 1983). Schlichter (1972) has shown that sea anemones produce more mucus when mechanically stimulated. An increase in the denstiy and activity of *D. sunnivae* may increase the amount of mucus produced by *U. lofotensis*, which may support a larger population of copepods.

Increased water temperature may be a positive factor affecting density for this species of copepod, but for the copepod *Paranthessius anemoniae* on *Anemonia sulcata*, density is inversely correlated with temperature (Briggs,1976). The reasons for this pattern are not known, but another factor which has been suggested to affect copepod population density on anemones is increased wave action during the winter months when there are more storms (Gotto, 1962; Lønning and Vader, 1984). Turbulent waters are assumed to affect the host location abilities of the larval copepods, thereby reducing recruitment. In Briggs' (1976) study, the copepod populations decreased during times of high wave action in winter. In the northeast Pacific, the number of storms increase throughout the fall period, and wave action could affect the populations of copepods. Decreased densities of copepods on anemones have been reported after heavy rain storms (Lønning and Vader, 1984), which suggests that salinity changes may also affect the survival of copepods on shallow water and intertidal anemones.

Predation by *O. pictus* had a large effect on the populations of *D. sunnivae* during the late summer and fall. The density of post-settlement *O. pictus* was negatively correlated with copepod densities, and anemones with associated fish had significantly fewer copepods than those without fish. Field and laboratory observations, combined with stomach content analysis, demonstrated that the fish were feeding on the copepods. Small post-settlement *O. pictus* removed most of the

D. sunnivae from the anemones, except in July when copepod population densities were rapidly increasing. Heavy recruitment of planktonic copepod larvae was likely taking place at this time, and the growth rate of the copepod populations appeared to be higher than the predation rate of the fish. The number of copepods on some of the host anemones increased from the July to the August survey even though associated fish were present during this period. In the fall however, when densities of small post-settlement fish increased, and individuals foraged over larger areas, there was a substantial increase in the predation pressure on the copepods. This may have resulted in the subsequent decrease in the population densities of the copepods.

The decline in copepod abundances during the fall of both years of the study was likely due to a combination of both predation and other physical factors. The results of the caging experiment demonstrated that even if *O. pictus* were prevented from preying on *D. sunnivae,* the populations of the copepods decreased over the fall period. This is also supported by the decline in copepod density in the fall of 1985 when the recruitment of *O. pictus* was very low. However, predation by *O. pictus* may be effective in maintaining *D. sunnivae* populations below their maximum density. This is suggested by the differences in population densities of the two species between the fall of 1984 and 1985. The density of *D. sunnivae* on the anemones was much higher during the late summer and fall of 1985 than during the same period of 1984. Conversely, *O. pictus* recruitment was much higher in 1984 than in 1985. These density patterns may not be causatively related, but they suggest that the high densities of small post-settlement *O. pictus* may have kept *D. sunnivae* populations below maximum densities in 1984, and low fish densities in 1985 allowed copepod populations to increase to higher levels.

Scyra acutifrons and other crabs

Scyra acutifrons was the most common crab species found with anemones. It benefitted from the association by receiving protection from predators, and by feeding on anemone mucus and food material. Large crabs (>2.5 cm) removed food material from the coelenteron of *U. lofotensis*, and they also appeared to scrape mucus from the tentacles of the anemones and move the material to their mouths. This type of feeding behavior is not uncommon for crab associates of cnidarians. *Mithrax commmensalis* is known to steal food from its host anemones (Stanton, 1979), and *Trapezia* crabs feed on the mucus of their coral hosts (Castro, 1976; Glynn, 1983). It is not known how much food material *S. acutifrons* obtains from anemones, but it probably makes up only a small proportion of the diet of most individuals.

Protection from predators is probably the major benefit that all the species of crabs received from associating with anemones. Many rockfish species were abundant at the study sites, and crabs are the most common item in the guts of some fishes (McElderry, 1979; J. C. Holmes, pers. comm.; pers. obs.). Octopuses also prey heavily on crabs (Hartwick et al., 1980). Small *O. rubescens* readily fed on *S. acutifrons* which were not associated with anemones during laboratory experiments. The anemones probably offered more effective shelter space than a crevice, since octopuses were able to enter crevices, but were repelled by anemones. The size of host anemones was important, and crabs were usually found with large individuals of *U. lofotensis*. Individuals of *S. acutifrons* were also commonly observed in aggregations of *Metridium senile* where the crab could hide between the columns of the anemones. Few crabs were observed with *U. piscivora* compared to their abundance with *U. lofotensis* and *M. senile*. This abundance pattern may reflect the differences in tentacle adhesion between the anemones. Crabs were able to contact the tentacles of *U. lofotensis* and *M. senile* without being stung, but they were captured and eaten by *U. piscivora*.

More crabs associated with anemones at Ohiat Islet than at Blackfish Islet. It is not known if this pattern is related to crab population densities since population surveys were done only at Blackfish Islet, but there are other possible explanations. *Scyra acutifrons* may utilize anemones more at Ohiat Islet because of higher predation pressure at this site and fewer physical refuges from predators. Changes in habitat utilization have been documented for other aquatic arthropods in response to fish predation pressure (Sih, 1982; Cook and Streams, 1984). Predatory fishes were more abundant at Ohiat Islet, especially *Sebastes nebulosus*. Stomach content analysis of *S. nebulosus* at Ohiat Islet (McElderry, 1979) revealed that 88 percent of the fish were feeding on crabs (*n*=33 fish) and 36 percent were feeding on spider crabs (which were assumed to be *S. acutifrons* since this is the most abundant spider crab at the site). Stomach content analysis of *S. nebulosus* by J. C. Holmes (pers. comm.) has also shown that this fish species feeds heavily on *S. acutifrons* and other crabs. The hard rock substratum at Ohiat Islet provided little shelter space for the crabs compared to the numerous rock boulder areas at Blackfish Islet. The lack of refuges may also explain why more crabs were associated with anemones in deep water at Ohiat Islet, since there were fewer sessile marine invertebrates and algae with which to shelter in this area compared to shallow water.

The crabs were nocturnally active, and more individuals were observed with anemones during the day than at night. This type of activity pattern is common for most marine crustaceans, and is usually related to the abundance and activity of diurnal predators (Castro, 1978). Predatory fishes fed most actively during the day and at twilight. The crabs benefitted most by associating with anemones at these times when they were easily detected by their visual predators. Mostly small crabs associated with anemones, probably because they are more vulnerable to predators than large crabs. At night, when predatory fishes were less active, the crabs were able to leave their shelter. Nocturnal predation by octopuses was probably less important than fish predation, since octopuses were rare compared to the predatory fishes at the sites.

Night-time activity of symbiotic crabs allows them to move between hosts, which is necessary for dispersal and establishment of mating pairs (Castro, 1978; Diesel, 1986). Females of the spider crab *Inachus phalangium* are known to be site-constant, but males move among anemones at night (Diesel, 1986). Individuals of *S. acutifrons* did not appear to have any fidelity to the same anemone host, and the crabs frequently moved between different anemones. It is not known if the crabs are territorial, and tagging and movement studies are needed to determine if they have distinct home ranges. Usually only one *S. acutifrons* was found per anemone, but no aggressive interactions were observed to suggest that there was any intraspecific competition for anemones. However, *S. acutifrons* did have a negative association (C8) with the other crabs ~~species~~ during day observations. This suggests there may be aggressive interactions determining which crabs are at a particular host.

There was a seasonal difference in the number of associated *S. acutifrons*, with more crabs being found with anemones in the late summer and fall. The significance of this pattern is not clear, but it may be related the generation cycle of the crabs, as has been shown for the spider crab *Inachus phalangium* (Diesel, 1986). Distinct size classes of *S. acutifrons* were not more abundant at different times of the year, but since crabs smaller than 0.5 cm were not reliably censused, patterns of recruitment and shifts in size class may have been overlooked.

Heptacarpus kincaidi

The shrimp *Heptacarpus kincaidi* is an associate of a variety of sea anemone species in different areas (Butler, 1980; Elliott, 1985), and is also known to occur in high population densities in deep water areas on soft substrata where anemones are not present (G. Shinn, pers. comm.; pers. obs.). Individuals of *H. kincaidi* were found only in the deeper areas of the survey sites (>7 m depth), sheltering in hydroid or bryozoan colonies, or with anemones. The shrimp were most abundant with anemones at Ohiat Islet, where many anemones were present in the deeper areas of the site (to 20 m). Predatory reef fishes are most abundant in relatively shallow water in Barkley Sound (<30 m) (pers. obs.), and many of these fishes feed primarily on benthic crustaceans (refer to discussion of predators). The shallow subtidal may be only a marginal habitat for *H. kincaidi*, and its utilization of this area may be facilitated by the presence of anemones which provide a refuge from predators. The red color pattern of this shrimp enables it to be very cryptic in deep water where red wavelengths of light do not penetrate (Butler, 1980), but in shallow water the shrimp were visible without the use of a diving light. They were probably more vulnerable to visual predators in shallow water. The shrimp were also hard to observe when next to the red columns of *U. lofotensis* and *U. piscivora*. However, *H. kincaidi* also associates with a white anemone, *Cribrinopsis fernaldi*. This species of anemone is mostly found in deep water (>25 m), and when shrimp are disturbed by a diver, they leave their host and quickly disappear from view.

Aggregations of many shrimps were observed around the column and under the tentacles of *U. lofotensis*. *Heptacarpus kincaidi* is not known to be territorial, and aggressive interactions were not observed between conspecifics. Many other species of symbiotic shrimps are territorial, and defend their host anemone against intruders (Bruce, 1976; Knowlton, 1980). Individuals of *H. kincaidi* did not appear to have any fidelity to one host anemone, and most shrimp probably moved between anemones during the night when they were most active (Elliott, 1985). The shrimp were only abundant on the anemones during July, August, and September of both years. The ecological factors responsible for this trend are not known.

General discussion

The previous discussion revealed that the number of associates found with anemones varied spatially, temporally, and with respect to the characteristics of different associates and hosts. The following discussion will identify the general patterns of this variation, and indicate how they may affect the costs and benefits to the partners in these associations. I conclude with an analysis of the evolutionary implications of this variation, and the conditions under which different types of associations may evolve.

Spatial variation

The population densities of the anemones and their associates differed between habitats. The frequency of associations between the organisms was therefore also different between areas. Blackfish Islet, Ohiat Islet, and the Harbor Limit differed with respect to wave exposure, the amount of structure in the habitats, and the density of predators (Fig. 26). These factors appeared to be most important in determining the population densities of the organisms at the three sites, which in turn, affected the number of associates found with the anemones. The number of organisms found with the anemones was related to the abundance of the particular species in the habitat.

Wave exposure had both direct and indirect effects on the population densities of the organisms. It had a positive effect on the population densities of *U. lofotensis*, *A. harringtoni*, *J. zonope*, and possibly *S. acutifrons* , but a negative effect on *O. pictus* and *C. nicholsii*. Depth modified the negative effects of wave exposure, and some species occupied the deep water areas in exposed habitats. Those associates which appeared to be well adapted to living in the same habitats as *U. lofotensis* were only intermittent associates with this anemone (except *D. sunnivae*). Those species whose overall distribution and abundance patterns were not similiar to *U. lofotensis* were

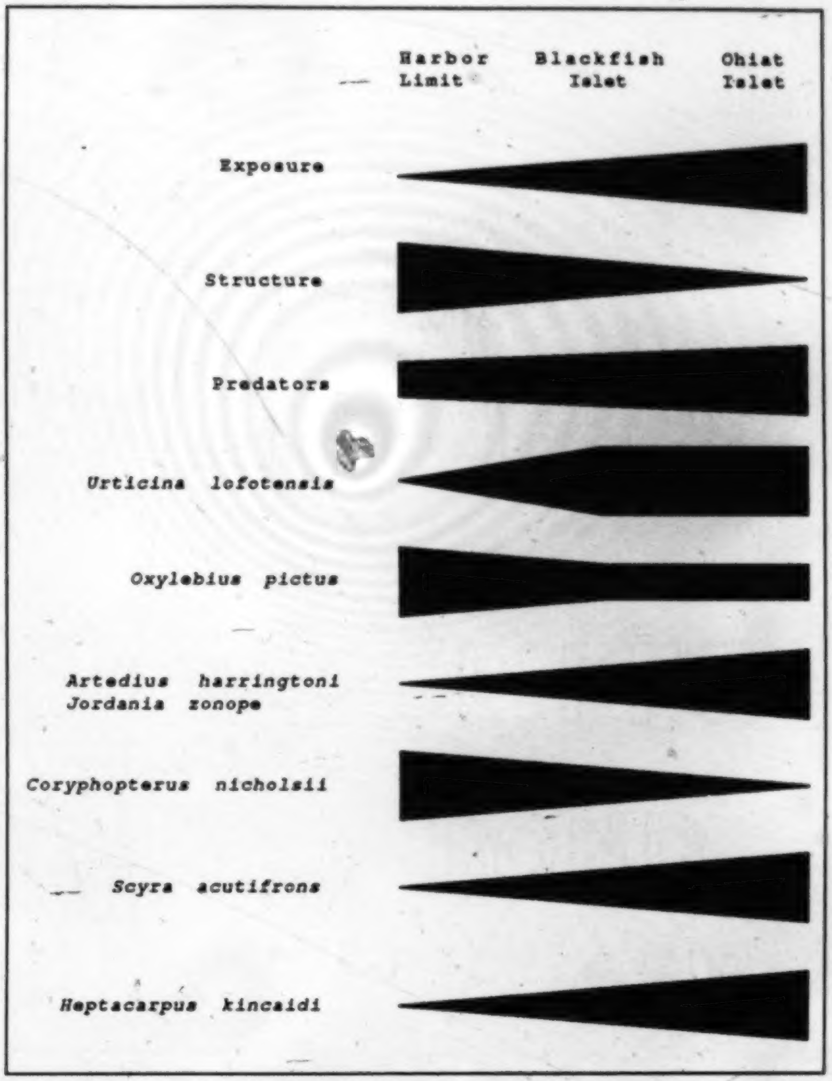

Figure 26. Summary of variations in environmental factors and population densities of anemones and their associates among the three study sites. Kite diagram represents high to low abundance or intensity of variable.

more closely associated with the anemones in areas where their distributions overlapped. This suggests that the associations were most important for the organisms which were outside of their normal range of environmental conditions.

Predation is very important in aquatic systems (Vermeij, 1984; Sih et al., 1985), and many authors have emphasized its importance in fish communities (Larkin, 1956; Helfman, 1978; Crowder and Cooper, 1982; Fraser and Cerri, 1982; Cowen, 1983). Predators should have an especially strong effect on prey of relatively small size (Connell, 1983; Schoener, 1983), and studies with fishes show that small individuals are most vulnerable to predators (Werner et al., 1983). Since most of the associates were of relatively small size in relation to their predators, and predators were abundant in the habitats, it is likely that predation was important in determining the distribution and abundance of the associates. Predation is implicated as the major factor controlling population density of *O. pictus* (DeMartini, 1976; DeMartini and Anderson, 1980), but no studies have addressed the question of population regulation of the other associates.

The species compositions and abundances of large fishes, which were predators of the associates (except copepods), differed between the three study sites. Large fishes were most abundant at Ohiat Islet, and were relatively less abundant at Blackfish Islet and the Harbor Limit, respectively (Fig. 26). This suggests that predation pressure on the associates was highest at Ohiat Islet, and lowest at the Harbor Limit.

The level of structure in a habitat, which provides refuges from predators, can greatly affect the foraging success of predators and subsequent persistence or abundance of prey (Sih et al., 1985). Crowder and Cooper (1982), and Gilinsky (1984) examined the influence of macrophyte density on the effects of bluegill predation on macroinvertebrate prey species. Both studies showed an increase in prey biomass with an increase in the level of structure in the habitat. Similarly, the persistence and absolute densities of the small fishes and crustaceans in this study may also be dependent on the amount of structure in the habitats (i.e., holes and crevices, and sessile invertebrates). The three study sites differed in the amount of physical structure, with the Harbor Limit having the most structure (boulders), and Ohiat Islet having the least (solid rock) (Fig. 26). The increased level of structure provided by anemones at the Blackfish and Ohiat Islet sites may allow *O. pictus* and *C. nicholsii* to better utilize these habitats, especially small post-settlement *O. pictus* which were highly vulnerable to predators when not sheltered. Shallow water is a marginal habitat for *H. kincaidi*, and anemones may also facilitate the presence of the shrimp in this area. The structural refuge provided by anemones was probably not as important to the other fish and large crustacean associates which also utilized crevices and other sessile invertebrates for shelter at Blackfish and Ohiat Islets.

Predation can profoundly affect the behavior of prey (Sih et al., 1985). Fish and arthropod prey have been shown to increase their use of refuges in the presence of predatory fishes (Frazer and Cerri, 1982; Werner et al., 1983; Cooper, 1984). Different levels of predation pressure have also been shown to possibly affect the frequency of the mutualistic relationship between hermit crabs and their anemones (Bach and Herrnkind, 1980). In the present study, there was no direct evidence of changes in behavior by the associates of *U. lofotensis* in areas of high and low predator abundance. However, further experimental studies of the association behavior of the fishes and crustaceans in the presence and absence of predators may demonstrate a difference in their patterns of habitat utilization.

Temporal variation

Predators affect the activity patterns of their prey (Sih et al., 1985). Large predatory fishes are most active during crepuscular periods when they have a visual advantage over their prey (Munz and McFarland, 1973; Ebling and Bray, 1976; Hobson et al., 1981). To decrease their chances of being eaten, most small fishes return to shelter before sunset and do not leave until after sunrise. These species usually remain inactive in their shelter areas at night, but they are also vulnerable to nocturnal predators at this time. In this study, the associated fishes were all diurnally active, and sheltered with anemones during twilight and darkness. The crabs and shrimp were all nocturnally active, and smaller numbers were found with anemones at night. Crabs, shrimps, and small fishes are the major prey items of the diurnal and crepuscular fishes (Moulton, 1977), as well as the nocturnal fishes (DeMartini, 1979), present at the study sites. The temporal variability in predation pressure by the fishes and octopuses was likely a strong selective force influencing the activity patterns of their prey. The associated fishes (except small post-settlement *O. pictus*) were able to escape most predators during the day, but they were probably vulnerable at night when inactive. The crabs and shrimp, which were less motile than the fishes, were probably highly susceptible to predation during the day when they were more conspicuous to visual predators.

There was a distinct seasonal trend in the abundances of all the associates with *U. lofotensis*. Highest numbers of associates were in the months from July to October, and there were few associates with anemones in the winter months. The population densities of the associates also varied through the seasons. These variations in density were related to seasonal changes in environmental conditions and recruitment.

Seasonal changes in the abundance of large fishes did not appear to determine the seasonal densities or association patterns of the symbionts. Predator densities were highest in the fall and lowest in winter and summer, which corresponded with that of their prey. The large fishes may actually be cueing in on the seasonal fluctuations in the densities of their prey, and be foraging most intensely in these areas at times of the year when prey are most abundant and are of small size from new recruits.

Densities of all the associates differed between years. Highest densities of all associates (except *D. sunnivae*) were recorded during the fall of 1984. Their numbers decreased throughout the rest of the study, with some species showing a small increase in the fall of 1985. There are no clear explanations for this pattern, except that 1985 may have been a bad year for recruitment. *Oxylebius pictus* had a relatively low recruitment of fish in 1985 compared to 1984. This may also be true for the other species. However, *D. sunnivae* populations were over twice as large in 1985 than in 1984, which suggests the factors causing the overall drop in densities of the other species did not affect *D. sunnivae*, or had a positive effect on the copepods.

Interactions between associates

Most of the species which associated with the anemones appeared to do so independently of the other species, as revealed by the many non-significant and low values of interspecific association (C8). There was no evidence of interspecific competition for hosts. The number of anemones was not limiting since less than 60 percent of the population had associates at times of peak density. The contrasting activity and association patterns of the fishes and crustaceans may have reduced the chances of interactions between these groups, and may act as a form of temporal partitioning of the host anemones. In the Caribbean, a small percent of the population of *Lebrunia danae* has associated fishes and crustaceans, and few aggressive interactions are observed between species (Stanton, 1979). In other tropical systems, interspecific aggression is often observed between obligate symbionts which attempt to occupy the same host (Preston, 1973; Fautin, 1984; Knowlton and Keller, 1986). However, in these situations the majority of the hosts are usually occupied. The shortage of this resource may cause increased competition between associates.

Predation by fishes on the crustacean associates of the anemones may be a more important factor affecting association patterns than has been shown by this study. Small post-settlement *O. pictus* had a large effect on the population densities of *D. sunnivae*, but the effect of larger fishes on the other crustacean associates was not clear. Co-occurrence patterns indicated that fewer *S. acutifrons* than expected co-occurred with *O. pictus* and *A. harringtoni* (Table 9). Also, no *H. kincaidi* were found on the same anemones as adult *O. pictus* during day or night examinations of the anemones. The only firm evidence of the fish feeding on the larger crustacean associates was from the stomach content analysis of *O. pictus*, but since both of these fishes fed heavily on crabs it is not unlikely that they would feed on small crabs which co-occurred with them on an anemone. All sizes of fishes were capable of feeding on the small juvenile stages of crustaceans, and megalops larvae were common prey items in the diets of both small and large *O. pictus*. These smaller stages were not adequately enumerated in this study, and their patterns of co-occurrence with fishes may be a better indicator of any negative interactions between these species.

There was also a significant positive association between *H. kincaidi* and *S. acutifrons*, but their C8 value was quite low. This co-occurrence pattern may be a result of the shrimp only being found in deep water, and the crabs also being common with anemones at these depths. *Heptacarpus kincaidi* also had a positive association value (C8) with the other crab species, but the biological significance of this result is unknown. The only negative association between the crustaceans was between *S. acutifrons* and the other crab species. This suggests that there may have been competitive interactions between these crabs for hosts during the day when the crabs were most abundant on the anemones.

Intraspecific interactions between associates were important in determining the abundance of fish associates on the anemones during the day, but not at night. The larger individuals of cohabiting *O. pictus* were observed to chase smaller individuals away from anemones during the day, and the small fish were able to return before sunset when the fish were becoming less active. Both associated sculpins and the goby are territorial (Hart, 1973; Moulton, 1977; Gascon, 1982; Eschmeyer et al., 1983), and during the day no two fish were observed with the same host. This is not surprising, since few fish associated with anemones during the day, but aggressive interactions used in the maintenance of territories may keep conspecifics from occupying the same anemone during the day. The crustacean associates did not display any intraspecific aggressive behaviors, and were often found with more than one individual on the same host.

Host specificity

The number of organisms which associated with a particular anemone was dependent on the size, shape, orientation, and tentacular adhesive force of the host. The fish, crab, and shrimp symbionts were most always found with large anemones (>6 cm), but copepods were found on anemones of all sizes. All seven species of anemones studied were able to reach fairly large sizes, but they all differed with respect to shelter space, and tentacle adhesion qualities. Since *U. lofotensis* had the most associates of all the anemone species at the study sites, it can be assumed that the characteristics of this anemone made it a better host than the others. Therefore, the qualities which appear to make a good host for a variety of associated species are: 1) large size relative to associates, 2) shelter space behind or within long tentacles, and 3) a relatively weak tentacular adhesive force which is effective at deterring predators, but not so strong as to seriously harm the associates. In the Caribbean, a variety of fishes and crustaceans asociate with *Condylactis gigantea* (Stanton, 1979; Hanlon et al., 1983), an anemone which has characteristics which are similar to large *U. lofotensis*. The associates of this anemone are also mostly facultative, and range from species which are able to contact the tentacles without being stung, to ones which hide in the spaces between the tentacles. Like *U. lofotensis*, *C. gigantea* has long tentacles which offer a large amount of shelter space, and it also has a relatively weak tentacular adhesive force (Levine and Blanchard, 1980).

Cost-benefit analysis

Roughgarden (1975) has presented a cost-benefit model to explain the conditions under which symbioses may evolve. The model is specifically used to illustrate the conditions under which a fish species may evolve from being a facultative commensal or parasite to an obligate mutualist of a particular species of host anemone. He defines the benefit of associating with anemones as the difference in fitness between an individual which has not attempted to colonize a host and an individual who has successfully found a host. Costs are defined as the difference in fitness between individuals which have not attempted to associate with anemones, and those which attempt to associate with anemones but fail to do so. Using these definitions, a simple cost-benefit analysis was done for each associated species and *U. lofotensis* (Fig. 27).

Most of the benefits arose from modifications of existing predator-prey relationships, and other benefits were through nutritional pathways to the associates. These are both common types of benefits in mutualistic and commensal systems (Addicott, 1984), and the main ways that cnidarians benefit their symbionts (Stanton, 1979). Protective benefits are indirect since they involve the presence of additional species besides the host and symbiont (Addicott, 1984). Associates which fed on the mucus or tissues of the anemones received direct benefits (Addicott, 1984). *Scyra acutifrons* also fed on the coelenteron contents of the anemones, and *O. pictus* fed on associated copepods. These were indirect benefits since they were modifications of existing predator-prey relationships.

The species which appeared to gain the most benefit from associating with anemones were *D. sunnivae*, *O. pictus*, and *H. kincaidi*. These species were probably highly susceptible to predators when they were not associated with anemones. This was experimentally demonstrated for small post-settlement *O. pictus*, but was assumed for the other species since the copepods were obligate

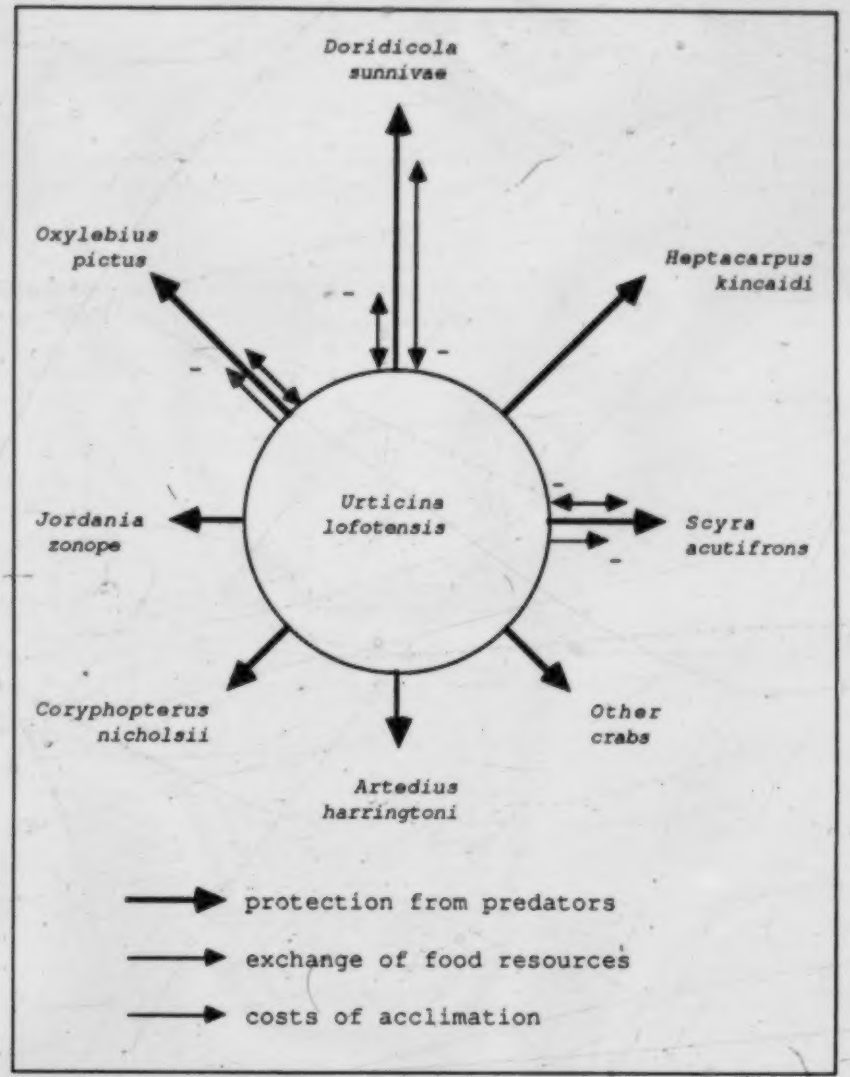
Doridicola sunnivae
Oxylebius pictus
Heptacarpus kincaidi
Urticina lofotensis
Jordania zonope
Scyra acutifrons
Coryphopterus nicholsii
Other crabs
Artedius harringtoni
-
-
-
-
-
protection from predators
exchange of food resources
costs of acclimation

Figure 27. Summary of the costs and benefits to the associates and *Urticina lofotensis*. Arrows indicate direction of cost or benefit. Lines with two arrows indicate that the interaction affects both organisms. Costs are indicated by a minus sign, benefits have no sign. The length of the lines refer to the magnitude of the interaction.

symbionts, and the shrimps were rarely observed without their hosts in areas where their distributions overlapped. Benefits were probably not as high for the other fish and crustacean associates which could survive in the absence of host anemones by sheltering in crevices and amongst other sessile invertebrates.

In Roughgarden's (1975) cost-benefit model, he assumes that the only cost to a symbiont is that of finding a host. It is clear that there are other costs to the fishes and crustaceans which associate with anemones. Any organism which attempts to associate with an anemone risks the chance of being stung, physically damaged, or captured if it contacts the tentacles of its host. If the associate is small in relation to the anemone (as in most cnidarian associations), then the symbiont may be able to avoid the tentacles of the anemone without getting stung (e.g., small reef fishes in the Caribbean; Hanlon et al., 1983). Relatively large associates must contact the tentacles of their host in order to adequately shelter themselves from predators (e.g., *O. pictus* and *S. acutifrons*). This requires a further investment in acclimation; physiological costs, tissue damage during early parts of acclimation, as well as the increased cost of being exposed to predators while acclimating (Stanton, 1979). These costs probably varied between anemones with different tentacle adhesion forces. Anemone fishes have been shown to differ in their ability to acclimate to different species of anemones (Mariscal, 1971; Lubbock, 1980; Brooks, 1981), which could possibly affect their selection of a host. Small post-settlement *O. pictus* were able to acclimate to *U. lofotensis*, but none of these fish were observed in the tentacles of *U. piscivora*, a species with strongly adhesive tentacles. Those fish which tried to associate with *U. piscivora* were captured and eaten. Crabs and shrimps which contacted the tentacles of *U. piscivora* were also captured and eaten. There is probably a lower cost for these associates to acclimate to *U. lofotensis*, which had a relatively weak tentacular adhesive force. Organisms capable of paying the costs of acclimation were also able to gain other benefits from the associations. Small post-settlement *O. pictus* were able to feed on copepods of the anemones, and *D. sunnivae* and *S. acutifrons* gained food resources from the anemones.

Symbionts must also locate their host in the habitat. The cost of finding a host will be higher in areas with low densities of anemones than in areas with high densities. Costs will also be lower for facultative symbionts than for obligate symbionts. Obligate symbionts, by definition, must find a host or they cannot survive. Facultative symbionts are susceptible to predators while searching for a host, but they can also utilize other shelter space if anemones are not available. In this system, the costs of finding a host were likely very high for *D. sunnivae*, but the high benefits of the association offset these costs. The only other symbiont which was likely to have any host searching behavior was *O. pictus*. In areas where *U. lofotensis* was present, small post-settlement *O. pictus* associated exclusively with anemones. However, these fish were also observed in areas where there were low densities of anemones or were absent, which suggests that the larvae of *O. pictus* search for anemones over a small spatial scale but will settle in areas without anemones if unsuccessful in finding a host. The amount of time spent searching for hosts would probably be quite small.

The potential costs and benefits to anemones of harboring associates were difficult to identify. None of the associates caused any apparent physical damage to the anemones, and the presence of associates did not affect the survival of their hosts. However, Lønning and Vader (1984) consider *Doridicola* spp. to be parasites of anemones. The copepods were observed feeding on the mucus and the tissues of their hosts, but this does not appear to be detrimental to the overall health of most anemones (Gotto, 1979; Humes, 1982). The presence of copepods may actually be beneficial to their hosts, as has been shown for the crustacean symbionts of corals (Glynn, 1976, 1983). Symbiotic crabs cause some tissue damage to their hosts, but the net effect of their presence is beneficial to the host. Further work is needed to establish the effects of the copepods on their hosts. *Scyra acutifrons* was occasionally observed picking at the tentacles of anemones, and stealing food from the coelenterons of some hosts. A loss of food is an obvious cost to the anemones, but since it occurs infrequently, it probably doesn't have a substantial effect on their fitness.

Anemones are suggested to benefit from their associates by receiving protection from predators, parasite removal, cleaning, and increased food resources (Mariscal, 1966, 1970). The only potential benefits which apply to this system are removal of copepod parasites, and cleaning provided by the copepods. These are obviously contradictory benefits. If the copepods are parasites, then the anemones benefit from the presence of *O. pictus*, which preys on the copepods. *Oxylebius pictus* and *U. lofotensis* would then have a mutualistic relationship. If the copepods are commensals or mutualists with the anemones, the status of *O. pictus* would change to a commensal or a parasite, respectively. More detailed studies are needed of the relationship between the copepods and their hosts to obtain a definitive answer as to the status of these associations. The other fish and shrimp associates of the anemones were probably commensals since they had no obvious detrimental effect on their hosts. Large *S. acutifrons* may be considered parasites since they stole food from anemones, but the majority of the associated crabs were small individuals which did not appear to feed on their hosts.

An important point to recognize is that the costs and benefits to the organisms varied over space and time, and between individual hosts and symbionts. Symbionts can shift from being a parasite to a commensal, to a mutualist, depending on the environmental (e.g., nutrient availability) and ecological (e.g., population density) conditions at that period in time (Addicott, 1984; Janzen, 1985; Whitfield, 1979). This variability makes it necessary to consider the costs and benefits to each individual over a variety of conditions, and use an average net measurement for the population to determine whether a species should be considered a parasite, commensal, or mutualist. This is obviously a difficult, and probably impossible, task for most associations. It is therefore difficult to apply these terms unless the costs and benefits are straightforward and relatively easy to measure.

Evolution of associations

Predation is seen as an important cause of selection in marine systems which favors the evolution of intimate associations between species (Vermeij, 1984). Since predators of the small fishes and crustaceans were abundant in this system, one would expect selection to favor the evolution of antipredatory adaptations in the prey. Because anemones are usually avoided by large predators, one would also expect them to attract a variety of vulnerable prey species. Roughgarden (1975) predicts that the initial formation of these associations should occur when the fitness of individuals which associate with anemones exceeds that of free-living or solitary individuals. He also states that three factors must occur for an association to evolve: 1) the host should be easy to find, 2) the host should survive well with the associate, and 3) the host should provide substantial benefit to the guest. *Urticina lofotensis* meets all three of these requirements of a host. The anemone is abundant, is long-lived in the presence of associates, and provides protection and food resources to associates. The simple change in shelter behavior required on the part of the associates for this type of antipredatory relationship to evolve may be reflected in the large number of small, free-swimming tropical fishes which shelter in the tentacular sphere of anemones, but do not come in contact with the tentacles without being stung (Hanlon et al., 1983). In this study, three small, common fishes species, *A. harringtoni, J. zonope, and C. nicholsii* also associated with anemones and avoided contacting their host's tentacles. The benefit to these species was probably low since they were able to survive adequately in the same habitats without anemones, but their costs were also very low.

The costs to *Heptacarpus kincaidi* were also low, but it appeared to benefit highly from associating with anemones in habitats where the shrimp was more vulnerable to predators. These simple behavioral modifications are considered to have preceded the further physiological and morphological adaptations needed to acclimate to sea anemones (Mayr, 1963; Gendron and Mayzel, 1976).

Those species which acclimated to anemones had higher costs, but they also had higher benefits. Small post-settlement *O. pictus* gained a substantial benefit from associating with *U. lofotensis*. The fish received necessary protection from predators, and the presence of copepods and other crustacean associates on the anemones may have been a further advantage for the establishment of the relationship; especially since larval fish settled out of the plankton at approximately the same time of year that *D. sunnivae* populations were at their highest densities on *U. lofotensis*. Predators were also most abundant at this time of year, which may increase the selective advantage of the association. By feeding on copepods the fish did not have to venture away from the protection of their host for food.

Doridicola sunnivae and *S. acutifrons* were also able to acclimate to the tentacles of *U. lofotensis*. The cost of acclimation must be relatively lower than the benefits for these organisms since associations with cnidarians have evolved in so many groups of crustaceans (Bruce, 1976; Gotto, 1979; Humes, 1982). The ability to contact the tentacles of the anemones allowed the crustaceans to feed on the mucus, tissues, and food material of their hosts. Roughgarden (1975) predicts that facultative associates which have the potential to harm their hosts should be more deleterious on hosts which have a high survival than on comparatively vulnerable hosts. The high survivability of *U. lofotensis* may promote the crustaceans to take advantage of the anemones by feeding on tissues or stealing food. If the detrimental effect of the copepods or the crabs significantly affected the fitness of *U. lofotensis*, one would expect the anemones to evolve some type of mechanism to inhibit the associations.

The anemones could either strengthen their defenses by increasing the adhesive force or toxicity of their cnidae, or they could make their mucus unpalatable to the symbionts. However, no evidence exists for any counter-adaptations on the part of the anemones in response to the presence of the associates.

Once a symbiotic association is established, there may be the potential for a mutualistic relationship to arise. For mutualism to be selected for, Roughgarden (1975) suggests that the symbionts must be highly dependent on their host for survival, and the survival of the host must be increased by the associated organism. Mutualisms may proceed much more readily if the initial conditions are neutral or commensal as opposed to parasitic (Keeler, 1985). This depends, of course, on if the symbiont has any attributes which allow it to confer some type of advantage to its host. If it requires no novel behavior or traits, or can be readily produced from existing genetic variation, then mutualism may be more readily established (Keeler, 1985). In this system, *D. sunnivae* has the potential to benefit the anemones through its normal feeding activities, if those activities involve cleaning the anemones of necrotic tissue or the larvae of other sessile invertebrates. In contrast, if the copepods are parasites of the anemones, then *O. pictus* may be a mutualist because of its normal activity of feeding on copepods. But, since *U. lofotensis* already has a very high survival rate, it appears that any mutualistic behavior by the associates would have a negligible effect on their host's survival.

Roughgarden (1975) suggests that facultative associations which confer large benefits to the symbiont while retaining high survival of the host should readily evolve into fully obligate relationships. This does not appear to be consistent with our present knowledge of the many species of fishes which are facultative associates of anemones (Hanlon et al., 1983). According to the assumptions of Roughgarden's model, these fishes either do not gain enough benefit, or the host has low survival on account of the presence of the associates, restricting them from developing an obligate relationship. However, it seems clear that other factors must also be taken in account before an association can become obligate. An obligate anemone fish cannot survive without being in close proximity to its host in order to escape from predators. Anemone fish feed mostly on planktonic prey, which allows these fishes to remain in the shelter of their host until a prey item passes by them in the water column. Facultative fish symbionts are not all planktivorous, and must leave the shelter of their host anemones in order to feed. If they are far away from their anemones it is necessary for them to retain the ability to escape predators. Therefore, the fishes' mode of feeding may determine their eventual dependence on their host anemones for survival. The only obligate associate of *U. lofotensis* was *Doridicola sunnivae*. The copepod not only received protection from its host, but by feeding on the anemone's mucus and tissues it never had to leave its host (except as larvae). This could lead to complete dependency on the host for food resources, and the inability to escape predators when away from hosts. *Oxylebius pictus* also received both protection and food resources from associating with anemones, but once the population of copepods was depleted, small post-settlement fish had to forage away from their hosts. The benefits also varied between different sized fish, and over space, time, and between hosts. This variability may also make it especially unlikely that an intimate association can evolve when there isn't constant selective pressure on all individuals in a population. Most symbioses are variable over space, time, and between individuals (Whitfield, 1979). Variations in the costs and benefits of symbiotic interactions need to be incorporated into models and our concepts of symbioses.

Intimate associations between between marine organisms are more prevalent in tropical regions than in temperate regions (Vermeij, 1984). This is especially evident for the tropical Indo-Pacific region, which has more obligate associations than other tropical areas. Obligate relationships between fishes and anemones are found exclusively in the tropical Indo-Pacific for two genera of fishes and five genera of sea anemones, but facultative associations do not show such biogeographic or phylogenetic boundaries. Obligate associations of crabs and shrimps with cnidarians are also more prevalent in the Indo-Pacific region than in other tropical and temperate areas. This zoogeographic pattern is suggested to be the result of decreased predation pressure and the greater variability in environmental conditions as one goes from the tropical Indo-Pacific region to higher lattitudes (May, 1976, Vermeij, 1984). In the tropics, where predation pressure is considered to be intense and relatively constant year round, there may be strong selection for obligate associations to evolve. In temperate regions, where predation pressure is less intense (Ebling and Bray, 1976; Hobson, et al., 1981; Vermeij, 1984) and varies seasonally, facultative associations may provide a more flexible means of increased survival. The previous discussion indicated that it likely requires more than intense predation pressure and constant environmental conditions for an obligate association to evolve. The trophic status of the symbiont, the types of benefits exchanged between partners, and the variability of the association are probably also important. Our knowledge of beneficial interactions is so incomplete and geographically biased that a satisfactory answer to this question cannot be reached with the presently available evidence (Vermeij, 1984).

The geographic distribution of obligate associations "may not reflect either the overall frequency or significance of mutualism" (Addicott, 1984). Other types of facultative associations must also be considered. Recent studies in marine ecosystems have shown that many beneficial interactions are less obvious because of reduced specificity (Vance, 1978), benefits being exchanged through indirect pathways (Duggins, 1981; Dethier and Duggins, 1984), or intermittent association (Shimek, 1981). The results of this study also show that some beneficial interactions are less obvious because of variability in the associations. Further investigations of interactions between organisms in the marine environment will probably reveal that symbioses are more prevalent in temperate regions than previously considered.

Plate 1. Concrete and rubber tubing model anemone used in field and laboratory experiments to test for whether *O. pictus* associates with anemones strictly because of their unique 3-dimensional structure.

Plate 2. Rubber model anemone used in field and laboratory experiments to test for whether *O. pictus* associates with anemones strictly because of their unique 3-dimensional structure.

Plate 3. Small post-settlement *Oxylebius pictus* (4 cm) on the oral disk of *Urticina lofotensis*.

Plate 4. *Oxylebius pictus* (10 cm) next to column of *Urticina lofotensis*.

Plate 5. Male *Oxylebius pictus* (10 cm) under the tentacles of *Urticina piscivora*. Male guarding egg mass (orange) spawned in colony of hydroids above the fish.

a)

b)

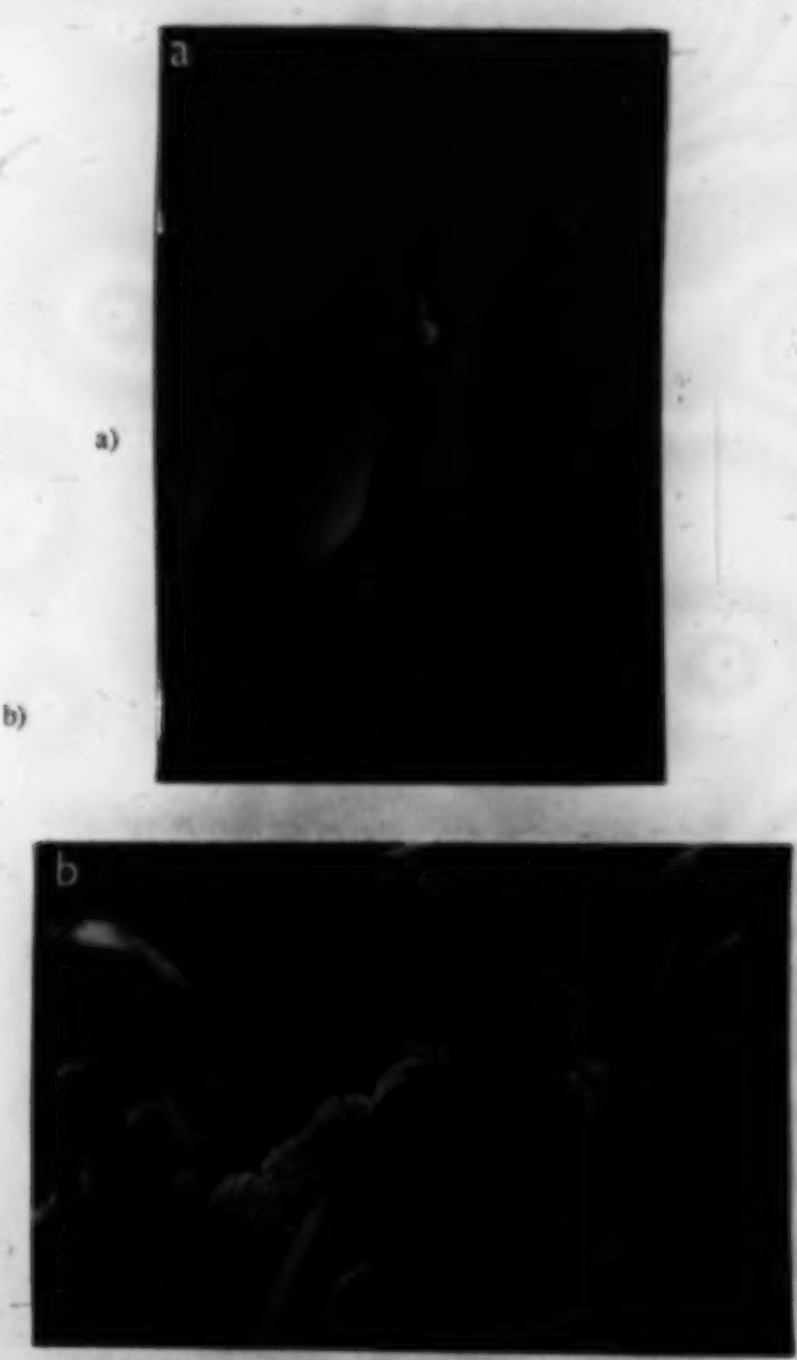

Plate 6. *Doridicola sunnivae* on the tentacles (a) and oral disk (b) of *Urticina lofotensis*.

Plate 7. *Scyra acutifrons* with *Urticina lofotensis.*

Plate 8. *Heptacarpus kincaidi* with *Urticina piscivora.*

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